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B. T. GALLOWAY, *Chief of Bureau.*

WILD WHEAT IN PALESTINE.

BY

O. F. COOK,

Bionomist in Charge of Crop Acclimatization and Adaptation Investigations.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., November 7, 1912.

Sir: I have the honor to transmit herewith a paper entitled "Wild Wheat in Palestine," by Mr. O. F. Cook, Bionomist of this Bureau, and to recommend its publication as Bulletin No. 274 of the Bureau series.

This paper contains a further account of the new cereal discovered by Mr. Aaron Aaronsohn, director of the Jewish Agricultural Experiment Station at Haifa, Palestine, and described by him in Bulletin No. 180 of this Bureau, entitled "Agricultural and Botanical Explorations in Palestine," which was published in 1910. The existence of a new type of wheat growing in a wild state was a matter of so much interest that Mr. Cook was instructed in 1910 to make a further investigation of the subject in connection with a visit to Egypt for the study of certain problems in the breeding of Egyptian cotton.

Though the present paper does not attempt to reach a final decision on the question whether the wild wheat of Palestine is the true ancestor or prototype of the domesticated varieties of wheat, it brings out several additional facts regarding the characters and habits of the plant, including the presence of specialized adaptations to facilitate cross-fertilization. This has an important bearing upon heredity and breeding because of the general theories and methods that have been based on the fact that many cultivated varieties of cereals have habits of self-pollination. The possibility that acclimatization and selection may develop improved varieties of the wild wheat worthy of cultivation for grain or forage is indicated by the results of an experimental planting in southern California. Another practical suggestion is the acclimatization of cross-fertilized forms of the domesticated type of wheat as a means of securing greater vigor, hardiness, and resistance to disease in the Southwestern States, where the self-fertilized European wheats often succumb to adverse conditions.

Respectfully, B. T. Galloway,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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WILD WHEAT IN PALESTINE.

INTRODUCTION.

Tracing the origins of cultivated plants is one of the most interesting branches of botanical geography. To learn where a plant like wheat was domesticated is to locate one of the milestones of human progress in remote prehistoric times. The adoption of fire and the domestication of plants gave primitive man an agricultural status and thus made possible the development of the other arts and institutions of human society. On account of the instinctive superstitious conservatism everywhere manifested among primitive peoples, it is reasonable to believe that the early stages of progress toward civilization were extremely slow and gradual and required many thousands of years.

That any definite knowledge is still to be gained regarding events that were forgotten long before human records began may seem quite impossible. But modern science finds methods of approach to many mysteries that were inaccessible to former generations. Space and time do not prove to be insuperable obstacles to scientific investigation. The astronomer projects his knowledge millions of miles into the heavens, to learn the motions and determine the composition of the stars. Biological relations of facts are as real, if not as definite, as the physical relations applied in the telescope and spectroscope.

The similarities of different species of plants and animals are not meaningless approximations or coincidences, but afford evidences of common ancestry and previous geographical association. It is as reasonable to look for related plants in adjacent regions as for related people in the same neighborhood. It is true that some species have been able to attain a very wide continental or cosmopolitan distribution, and especially those that have taken advantage of human assistance, like the weeds that infest cultivated lands. But even such plants usually have localized relatives from which the original center of distribution may be learned.

In addition to their historical and ethnological interest, the wild relatives and ancestral forms of our cultivated plants are also of practical value in relation to agriculture. Unless the ancestral form and wild relatives of a domesticated species are known it is impossible

to understand what the effects of breeding and cultivation may have been or to determine the possibilities of further improvement.

The wheat plant has served as the chief example of reproduction by self-fertilization. Many writers on heredity have considered self-fertilization as a normal condition and have made it the basis of general theories of heredity. Methods deduced from such theories have been widely recommended for the breeding of varieties of plants and animals, and even for the improvement of the human race.

The chief object sought in studying the behavior of wild wheat under natural conditions was to learn whether it was adapted to cross-pollination or limited to fertilization by its own pollen and whether there was natural individual diversity (heterism), as in other wild plants, or uniformity, as in self-fertilized or artificially selected varieties.

The present report is based on observations of wild wheat in its native habitat in the months of June and July, 1910. The visit to the wild-wheat country was made in connection with an investigation of cotton culture in Egypt, as reported in a previous publication.[1]

The season proved to be too far advanced to afford a really favorable opportunity for the study of the wild wheat, and the time that could be devoted to this purpose was too short to make any complete study of the facts that could still be observed. Nevertheless, it was possible to secure quite definite evidence on the chief questions. All doubts of the status of the plant as a normally cross-fertilized wild species were resolved. This was shown, not only by the wide range of individual diversity, but by the presence of several specialized adaptations to facilitate cross-pollination.

In addition to the description and discussion of facts observed during this visit to Palestine, several further observations by Mr. Aaronsohn are included in the present paper. Any such examination of the wild wheat in the short time available would have been quite impracticable without the advantage of his previous study of the plant [2] and familiarity with the country, to say nothing of the hospitality and facilities of travel provided by him and his family.[3]

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[1] Cook, O. F. Hindi cotton in Egypt. Bulletin 210, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1911.

[2] Aaronsohn, A., and Schweinfurth, G. Die Auffindung des wilden Emmers (*Triticum dicoccum*) in Nordpalästina. *In* Altneuland Monatsschrift für die Wirtschaftliche Erschliessung Palästinas, Berlin, July–August, 1906, nos. 7–8, p. 213–220.

Contribution à l'histoire des céréales. Bulletin de la Société Botanique de France, vol. 56, 1909, p. 196–203, 237–245, and 251–288.

Agricultural and botanical explorations in Palestine. Bulletin 180, Bureau of Plant Industry, U. S. Dept. of Agriculture. August, 1910.

Wild dry-land wheat of Palestine and some other promising plants for dry farming. The Dry Farming Congress Bulletin, vol. 3, no. 3, Feb. 1, 1910, p. 161.

See also Schweinfurth, G., Ueber die von A. Aaronsohn ausgeführten Nachforschungen nach dem wilden Emmer (*Triticum dicoccoides* Kcke.). *In* Berichte der Deutschen Botanischen Gesellschaft, vol. 26a, pt. 4, 1908, p. 309–324.

[3] Mention is made in footnotes of a few recent observations by Mr. Aaronsohn, communicated during a visit to Washington while this bulletin was being printed.

BIOLOGICAL SIGNIFICANCE OF WILD CEREALS.

A special interest may be claimed for the biology of the wheat plant since no other plant can be said to have had so great an influence on the theory and practice of breeding. In what other line of plant breeding can any such series of notable successes be enumerated as those of Le Couteur, Sheriff, Vilmorin, Hays, Garton, Spillman, Nilsson, Tschermak, and many others who have developed new varieties of wheat and new refinements of the art of selection? Indeed, it might almost be said that plant breeding is based on the wheat plant, since a very large part of the interest in breeding relates either directly to the improvement of wheat varieties or to the application of the same methods to other plants. Even general theories of plant breeding seem to have been deduced largely from the biology of the wheat plant.

As long as no wild prototype or close relative of the wheat plant was known, it could be maintained that the habit of strict self-fertilization, as shown in cultivated varieties of wheat, represented the normal method of reproduction. Uniform self-fertilized strains of wheat and other cultivated plants have accordingly been considered by many investigators as representing the true nature of species and used as standards of judgment in the further study of the factors of heredity and evolution.

If each uniform variety is to be looked upon as a distinct elementary species it is equally logical to consider each abrupt mutative variation that comes true to seed as representing the origination of a new species. These ideas form a part of the theory of evolution by sudden mutative changes of one species into another, which some modern writers on heredity would substitute for Darwin's idea of evolution by gradual changes of the characters of species.

With a plant as definitely restricted to self-fertilization as the cultivated varieties of wheat are supposed to be, the tasks of individual selection, testing of progenies, and increase of superior strains are reduced to an ideal simplicity. When cross-pollination is prevented by the structure and habits of the plants the difficulties of isolating varieties to prevent crossing in the field do not arise. Different varieties and individual selections from the same stock may be planted side by side without danger of crossing, and the same plantings may serve the double purpose of breeding and testing. The only precaution is to avoid the admixture of different stocks of seed.

But with cross-fertilized plants, like Indian corn or cotton, the methods that have been used for wheat breeding are entirely inadequate. Each stock must be isolated, either by planting in a separate place where the pollen of other varieties will not be carried by the wind or by insects, or artificial pollination must be performed and

foreign pollen excluded. Without these additional precautions the methods of breeding that improve the wheat crop are entirely inadequate, or even dangerous, when applied to superior strains of cross-fertilized plants. To overlook the difference between self-fertilized and open-pollinated plants not only permits inadequate general theories to be framed but leaves out of account some of the most serious difficulties in breeding.

The convenience of self-pollinated plants for breeding experiments should not be taken as proof that restriction to self-fertilization represents a normal biological condition. The preponderance of biological evidence indicates that the crossing or uniting of different lines of descent has a physiological function in maintaining vigor and fertility.

Some writers have supposed that plants like wheat constitute a separate class where crossing does not have its usual significance and self-pollination is the normal condition. Breeders and students of heredity are divided between three general theories or schools of opinion—one which accepts self-fertilization as the normal and ideal condition, another which accepts cross-fertilization, and a third which accepts both conditions and advocates a dualistic or double theory, crossing being assumed as normal for some plants but not for others. The wheat plant has served thus far as the most important example of self-fertilization. For this reason the habits of pollination of the wild relatives or ancestral types of wheat command a general interest in relation to the whole philosophy of heredity, as well as a special interest in relation to the breeding of this most important cereal.

The wild prototypes and relatives of wheat are also likely to have direct value for breeding purposes. Crossing these with our domesticated varieties may be expected to lend increased vigor, hardiness, or other desirable characters. Other possibilities lie in the direction of acclimatization or domestication of new forms that are more desirable or better adapted to particular conditions. It is not surprising that European varieties of wheat should not thrive in our Southwestern States. The selective improvement of a variety in England, France, or Germany might reduce or exclude the very characters that would be needed to adapt the plant to our Southwestern conditions. It is not to be supposed that primitive man chose in all cases the best plants for domestication or that the forms that happened to be selected are the best for our present needs.

A GENUINE WILD WHEAT IN PALESTINE.

One of the chief difficulties in tracing the origins of cultivated plants arises from the fact that many domesticated species have escaped from cultivation and resumed their wild state in different parts of the

world, often in regions remote from their original habitats. In as old a country as Palestine there certainly has been no lack of opportunity for wheat to escape from cultivation and establish itself as a wild plant, if it were capable of doing so.

Though the total area of cultivation was probably greater in some of the more prosperous epochs of former times, wheat is still grown over nearly the whole country. The natives often climb to remote and almost inaccessible places to plant a few square yards of wheat. The deserted courts and chambers in the ruins of the fortress of Cæsarea Philippi on the pinnacle of a mountain spur above Banias are still planted every year with wheat in much the same way that the Indians of Central America use the terraces and walled inclosures of the ruins of Rabinal, Quiche, and Ocosingo for the planting of corn. The soils about these ancient ruins seem to have a perennial fertility, either because they represent the débris accumulated by former populations or because of exceptional natural fertility that attracted the primitive inhabitants and favored the development of centers of civilization in ancient times.

The native methods of harvesting and carrying home the unthrashed wheat on the backs of donkeys and camels are well calculated to scatter the seed along all the footpaths of the country, and this probably accounts for the frequent occurrence of apparently spontaneous plants of the domesticated type of wheat. A little careful searching in almost any locality is likely to reveal the existence of scattered wheat plants growing spontaneously by the roadside. This is true of the districts where the wild wheat abounds, as well as of other parts of the country.

Yet there is not the slightest indication that the wild wheat owes its existence to this scattering of the seed of the domesticated wheat. In spite of abundant opportunities it does not appear that domesticated wheat has anywhere made good its escape from cultivation. It is not known in any place as a genuine wild plant, but usually remains limited to the roadsides and to lands recently cultivated, being unable, apparently, to hold its own in competition with native vegetation.

The wild wheat, on the other hand, not only maintains an existence without any human aid, but occupies large areas altogether too rocky and broken to admit of agricultural occupation. (See Pls. I and II.) In such places it often appears as the dominant grass, showing itself abundantly able to hold its own in competition with other forms of vegetation. This supremacy may be explained, at least in part, by the specialized adaptive characters that are to be discussed in a later chapter of this bulletin.

The possibility of the wild wheat representing an escaped form of the cultivated wheat was also considered from the standpoint of

heredity. Spontaneous plants of the domesticated type of wheat were examined at every opportunity, and specimens collected and compared to see whether they showed any approximation to the wild type. No indication was found that the domesticated wheat when growing spontaneously, even under the most unfavorable conditions, has any tendency to revert toward the characters of the wild plant. (See Pls. III and IV.)

Nor does the wild wheat, when it finds more prosperous conditions in cultivated fields, show any tendency to lose its distinctive peculiarities and take on those of the cultivated wheat. The plants become much more luxuriant, with wider leaves, more numerous stalks, and larger heads than are usually shown in uncultivated land, but the essential differences of structure and habits are not lost or even appreciably diminished.

The determination of the status of the plant as a genuine wild species is entirely distinct from the question whether the wild wheat represents the true ancestral form or prototype of domesticated sorts. That the plant is a true wild species can hardly be doubted by anyone who has observed its characters and habits of growth under its native conditions and compared them with those of the cultivated and spontaneous forms of the domesticated species. A final solution of the prototype problem requires a different kind of evidence. As Mr. Aaronsohn has pointed out, the characters of the wild wheat of Palestine correspond in a remarkable manner to those that had been predicted for the prototype of cultivated wheats by Koernicke and other eminent authorities in the study of the cereals. Yet much experimentation with and study of both wild and cultivated wheats may be necessary before the prototype question can be definitely settled.

The prototype question becomes all the more interesting because the existence of a genuine wild type of wheat in Palestine can be certified. If the Palestine wheat can be accepted as the prototype, it will make possible a most interesting and important determination of the extent to which the characters and habits of the wheat plant have been modified in domestication. On the other hand, if the Palestine plant is not the true prototype of domesticated wheat, but an independent species, it will still have very great scientific and practical interest as the nearest collateral relative of cultivated wheat thus far known in a wild condition.

Specialists in the study of cereals may consider it desirable to describe the Palestine plant as wild emmer instead of as wild wheat, but this is calculated to obscure the true interest of Mr. Aaronsohn's discovery. "Emmer" is not an English word and can be made intelligible to the general reader only by defining it as a kind of wheat.

Spelt also is always considered as a type of wheat, though it has less similarity than emmer to the more familiar forms of wheat. There is no word but "wheat" to serve as a general name for the cereal grasses that belong to the genus Triticum.

To call the wheat "wild emmer" is also misleading, or at least premature, for it involves the idea that the wild plant of Palestine is to be associated definitely with emmer and not with other kinds of wheat, which has not been shown and may not be true. Koernicke's changes of botanical treatment in identifying the wild plant first with the einkorn wheat (*Triticum monococcum*) and then with the emmer wheat (*Triticum dicoccum*) shows how uncertain he was regarding the true affinities of the new type, which probably belongs to neither of these species. Both the emmer and the einkorn lack the most characteristic features of the wild wheat, the elongated kernels and the lateral articulations of the joints of the rachis. The articulation of the wild wheat is the most specialized of any of the plants in question. The narrowed base of the joint is not attached at the end, as in emmer and einkorn, but on one side, as in the wild barley. The joints of emmer not only break off at the end, but the point of insertion into the next joint below is in a distinct pit, the outer rim of which is produced into a broad, angular tooth, not present in the wild wheat.

In view of the fact that the Palestine plant has a definite status as a wild species, it would have been better to give it an independent specific name than to treat it as a mere varietal appendage of a domesticated form. The presence of two seeds in the spikelets, which suggested Koernicke's name *dicoccoides*, is a superficial and variable character, and the subspecific name *dicoccoides* becomes absurdly tautological when used in the combination *Triticum dicoccum dicoccoides*. It is fortunate in such a case that the rules of botanical nomenclature do not require the retention of the previous varietal name when a plant is recognized as a distinct species. This makes it possible in the present instance to avoid further misunderstanding by giving the wild wheat of Palestine an independent specific name. For this purpose the new name *Triticum hermonis* is suggested, to commemorate Mr. Aaronsohn's discovery of the plant in the region of Mount Hermon.

ADAPTATIONS FOR CROSS-FERTILIZATION.

EXSERTED ANTHERS AND OPEN GLUMES.

Though self-fertilization has been generally accepted as the normal habit of the wheat plant, some observers are inclined to think that natural crossing may take place frequently, either by insects or by

wind-borne pollen. Though the flowers are not visited by bees or other large insects that carry pollen for other plants, the general presence of thrips in wheat flowers forbids any general assumption of a total absence of cross-pollination, as pointed out by Mr. Luther Burbank in conversation several years ago. It is conceivable that in the natural home of the wheat plant thrips or some other small insect might act as a regular agent of cross-fertilization. Although this would represent a very specialized condition in a member of the grass family, it would not appear as improbable from a general biological standpoint as the complete absence of crossing that some writers have been willing to assume.

In Palestine, as in the United States, thrips is a very common insect in the wheat fields and could reasonably be expected to carry occasional grains of pollen from one flower to another. But in Palestine it does not appear that either the wild or the domesticated wheat is dependent on thrips or other insects for cross-pollination, for both plants share the ability of other wind-pollinated grasses to extrude the anthers and expose the stigmas. The extrusion of the anthers scatters pollen upon the wind and the spreading of the glumes admits pollen to the receptive stigmas.

That the stigmas do not project outside the glumes is not to be taken as an evidence against cross-fertilization, but is rather to be considered as an adaptation to favor crossing in a desert climate where pollination is often endangered by the shriveling of stigmas by dry winds. Thus the drying of the silks before fertilization can take place is one of the chief difficulties in the production of Indian corn in dry climates. The stigma of the wheat plant is a very delicate, many-branched, mosslike structure that requires protection from drying, but is extremely well adapted to catch any grain of pollen that may fall into the chamber where the stigma lies hidden between the protecting glumes.

With the glumes of the wild wheat in their usual closed position the chance of a wind-blown grain of pollen falling in between them would be very small, and at first it did not appear that any large quantity of pollen was available for distribution by the wind. Though many extruded anthers were visible, examination with a lens showed that most of them were completely empty. Many of them belonged to flowers whose stigmas had evidently been fertilized several days before, for the seeds were already well developed. In some cases it seemed that the empty anthers were being pushed out from between the glumes by the elongation of the young kernels. The finding of well-developed seeds in spikelets that had never emerged from the inclosing sheath also showed that the wild wheat, as well as the domesticated, is undoubtedly capable of self-fertilization.

Wind pollination, it seemed, might be a very small factor, notwithstanding the exsertion of the anthers.

But such inferences would have been erroneous, because the first observations were made too late in the day. When a better opportunity was finally secured, so that a study of the behavior of the wild-wheat flowers could be made early enough in the morning, a very different impression was gained. Some of the plants showed many freshly extruded anthers hanging on long filaments and just beginning to scatter their pollen. On other plants there were flowers with the glumes spread wide apart, ready to receive the pollen. The glumes separate at angles of about 30° or 40°, forming a broad tube or funnel with the expanded stigma at the bottom. Though well protected on all sides, the stigma can be seen by looking in from above. (See Pl. V.)

In other cases young, unripe stamens were found in open flowers along with apparently adult, receptive stigmas. These flowers were obviously proterogynous, the stigmas being ready for fertilization well in advance of the ripening of the stamens. Two pollen grains were seen on the branches of the stigma of one of these open flowers whose anthers were still very young and green. Though it could not be certified that the grains were wheat pollen, their presence left no doubt that the stigmas were accessible to pollination from adjacent wheat plants whose exserted anthers were then scattering pollen. The production of very regular, well-filled seed heads may also be taken as an indication that cross-pollination is usually accomplished, though there is a possibility that the stigmas of proterogynous flowers remain receptive long enough to enable them to be fertilized from the anthers of the same flowers, in the event that no foreign pollen arrives.

Students of flower pollination have long been aware of the fact that the opening of the glumes makes it possible for the flowers of the wheat plant to be cross-pollinated.[1] But breeders and writers on heredity have taken little account of such facts, perhaps because most of them lived in northern climates, where cold or wet weather often prevents the opening of the flowers. The possibility that cross-fertilization might represent the ancestral condition has not been considered.

The finding of what appears to be a natural hybrid between wild wheat and Aegilops may be considered as a further indication that natural conditions are not unfavorable for crossing. Aegilops is another grass that was formerly considered by some writers as the wild prototype of wheat. As one of the species, *Aegilops ovata*, has been crossed artificially with domesticated wheat, some botanists

[1] Knuth, P. Handbook of Flower Pollination, translated by Davis, vol. 3, p. 529.

FIG. 1.—Young head of wild wheat with exserted anthers. (Natural size.)

unite Aegilops with Triticum instead of treating it as a distinct genus. Only a few spikelets of the supposed hybrid were found, and these all in one spot, very likely from the same parent plant. Mr. Aaronsohn considers them as undoubtedly representing a hybrid, an opinion which his long familiarity with the wild wheat and the Syrian forms of Aegilops would give him the best of qualifications to pronounce. The characters of the hybrid are definitely intermediate in the structure of the head, the rachis, and the beards, as well as in the characters of the spikelets themselves.[1] (See Pls. VI and VII.)

INDICATIONS OF SEXUAL DIMORPHISM.

That the wild wheat plant may be dimorphic with reference to the behavior of the stamens and anthers is a possibility worthy of consideration in further investigation of this subject. At the end of June the season was too far advanced to permit an adequate study to be made, for nearly all the plants had passed beyond the flowering stage. It was only in cases where the wild wheat had invaded cultivated lands and was able to produce large, many-stooled plants that there were enough young heads to serve as a basis of comparison of the behavior of different individuals in these respects. In two or three places where such comparisons were possible it was noticed that on some plants all of the young heads showed pendent, exserted stamens. (Fig. 1.) Other plants showed no well-exserted stamens, but only such as might have been pushed out by the elongation of the developing pistil. The former may have represented a proterandrous caste, the latter a proterogynous or autogamous caste. At least, these differences indicate a wide range of variation in the relative age and time of maturity of the stamens and pistils.

One spikelet with open glumes was found on a head of wild wheat that did not appear to be very young, but the stigma was still fresh, as though

[1] Reference is made by Mr. Aaronsohn to the so-called *Triticum aegilopoides*, a natural hybrid found in the vicinity of Montpellier, France, as described by Fabre, Godron, Jordan, and others. See also Bally, W., Chromosomenzahlen bei Triticum- und Aegilopsarten, ein cytologischer Beitrag zum Weizenproblem, Berichte der Deutschen Botanischen Gesellschaft, v. 30, p. 163, 1912.

this spikelet were waiting for fertilization. Other young heads of the same plant did not show any spreading glumes, but it was found that some of the younger heads would spread their glumes as soon as the plants were pulled up. The change of position required only a moment, so that it was possible to see the glumes open.

The visible spreading and closing of the glumes when the plants were pulled left no doubt, of course, that these organs are capable of motion or that they can change their position promptly, to take advantage of special conditions. The plant is evidently possessed of a mechanism that causes the glumes of flowers of the right age to open, doubtless as a result of some particular condition of internal pressure or turgor. The favorable condition is very soon passed and the glumes are closed again. If the opened heads are dropped into alcohol they open still farther, but close up later on. Only in a few spikelets that were put under immediate pressure was it possible to secure any permanent illustration of the open position. (Fig. 2.)

FIG. 2.—Open spikelets of wild wheat, showing the position of the parts at the time of flowering. (Natural size.)

The power of motion is evidently confined to glumes in certain stages of development. Very young heads containing small immature anthers did not open their glumes with other heads of the same plants, nor did older heads with grains that had grown to about half the adult length. But some of the heads that opened their glumes when the plants were pulled had undoubtedly passed the stage of fertilization. The glumes of the lower spikelets of a head would sometimes open when those of the upper spikelets did not, the lower being less advanced in development.

Though the power of motion evidently does not cease entirely at the time of fertilization, it is undoubtedly present during that period, and enables the plants to take advantage of brief periods of time when the conditions are most favorable for cross-pollination, doubtless depending on air temperature and humidity. These factors must be greatly influenced by exposure, in a region so broken as the wild-

wheat country about Mount Hermon. As nearly as could be judged from limited opportunities of observation, the shedding of the pollen and the opening of glumes seem to occur within a short time, perhaps not more than half an hour after the plants have been exposed to the light and warmth of the morning sun; that is, the period of the drying of the dew, which is not heavy on the denuded slopes, where most of the wild wheat grows.[1]

It has been observed by Mr. J. B. Norton, of the Bureau of Plant Industry, that the flowers of rye are sensitive to mechanical irritation and can be induced to open by slight rubbing with the hand. The same may be true of the wild wheat, and may account for the opening of the glumes on the plants that were pulled up. Under natural conditions a mechanical stimulus would be applied when the awns are shaken by the wind. A breeze that would bring pollen to the flowers might at the same time afford the stimulus for opening the flowers to receive the pollen. If the awns serve in this way as a part of the mechanism for opening the flowers another remarkable specialization must be added to the list of cross-fertilizing adaptations among the wild cereals.

ANALOGIES WITH DOMESTICATED WHEAT.

The specialized adaptations of the wild wheat should be taken into account in attempting to understand the status of domesticated varieties with reference to cross-fertilization. Whether the wild wheat of Palestine be considered as the prototype of the domesticated wheat or not, it is reasonable to look upon its habits as affording the best analogy with those of the ancestral form of the cultivated wheat. The condition of self-fertilization in the cultivated varieties involves the loss of some of the specialized features of the wild plant, such as the exsertion of the anthers and the spreading of the glumes. The awns also seem to be quite without function in the self-fertilized varieties, many of which are awnless. That these characteristics should have disappeared equally from all of the very numerous cultivated sorts would not be expected and is not the case.

Some of the forms of cultivated wheat of Palestine still share the habit of cross-fertilization with the wild wheat. This was definitely indicated by the finding of heads of cultivated wheat with the glumes spread like those of wild wheat in the same district where the wild wheat grows, on the slopes of Mount Hermon, above Arny. It was near the upper limit of wheat cultivation, the only place where the

[1] Mr. Aaronsohn has observed that the dew is sometimes quite heavy, but that on such days the glumes remain closed, or open for only a very short period, probably because the air is already too dry and the temperature too high by the time the dew has evaporated. Near the coast the opening of the glumes takes place between 7 and 8 o'clock in the morning and from 5 to 5.30 in the afternoon.

cultivated wheat was seen in the flowering stage. A few days before several spontaneous plants of domesticated wheat had been seen near El Hadr with many exserted anthers. The plants that showed the open glumes were vigorous individuals, growing close to an irrigation ditch. Both plants belonged to the same general type, which may be considered as a primitive form of the domesticated species in view of the apparent retention of the habit of cross-fertilization. The glumes of the domesticated wheat were open early in the morning, as in the wild wheat.

In a recent report on the crossing of wheat in India the suggestion is made that cross-fertilization takes place when the glumes are opened by the wilting of the plants in the middle of the day.[1]

ADAPTATIONS FOR DISSEMINATION AND GERMINATION.

STRUCTURE OF RACHIS AND SPIKELETS.

Though domesticated plants are superior to wild species from the standpoint of utility to man, this superiority often involves a loss of some of the specialized characters that were of use to the plants in the wild state. From a biological viewpoint the wild wheat appears superior to the domesticated plant in its adaptations for protection and sowing of the seed, as well as in its better provision for cross-fertilization.

In the discussion of cereals from the agricultural standpoint the difference between the heads of wheat and barley is usually described by saying that barley has a fragile or brittle rachis, but this expression seems inadequate to describe the fact for biological purposes. The rachis of the wild wheat as well as of wild barley is not merely brittle in the sense of being broken easily, but is provided with

[1] "It will be evident from the above that natural crossing in wheat is far more frequent under the conditions obtaining on the canal colonies of the Punjab than it is in Bihar. At Pusa five cases have been proved. Two hundred and thirty-one cases were proved by us at Lyallpur, and of these no less than 226 took place in 1907. In the dry climate of the Chenab colony, wheat is grown entirely by canal irrigation and is usually watered at least twice after sowing, the last watering taking place after the plants are in ear. Often before this last irrigation the supply of water in the soil is so small that the plants wilt during the hottest part of the day, the glumes open, and the stigmas are exposed to the air. Under such circumstances, in the dry, hot climate, natural crossing is easy and it is not surprising, therefore, that it is so frequent. Experimental cultures might be protected to some extent from natural crossing by more frequent and even watering. Wheat breeding will always be very difficult at Lyallpur, and it will be necessary to bag the F_1 generation at least. Pure line cultures will have to be rogued every year and frequently reselected, and the trouble and difficulty of growing pure seed for cultivators will be considerable.

"In the damper climate of North Bihar, where wheat is grown without irrigation on high-moisture-retaining loams, natural crossing although occurring gives little trouble in selection and breeding work.

"It will be evident that the environment may modify to a considerable extent the usual pollination mechanism in a crop. In northern Europe cross-pollination in wheat is a rare occurrence; in warmer climates it is more frequent; while in hot, dry localities, such as the canal colonies of the Punjab, where the crop can only be grown by means of artificial irrigation, cross-pollination is quite common." See Howard, A., Howard, Gabrielle L. C., and Khan, Abdur Rahman, "The economic significance of natural cross-fertilization in India," Memoirs of the Department of Agriculture in India, botanical series, vol. 3, no. 6, October, 1910, p. 302-303.

specialized articulations that separate of their own accord at maturity. Moreover, the joints are not only constructed to fall apart from each other at maturity, but to remain firmly attached to the spikelet. The joint becomes, in effect, the beak of a spikelet, rendering that organ much more efficient for carrying the seed and burying it in the ground.

The utility of the joints of the rachis as beaks for the spikelets is greatly increased by the fact that they are barbed along the edges and at the upper end with long, stiff bristles. Thus, with respect to the rachis, there appear to be two distinct differences between the wild wheat and the domesticated. The wild wheat has the rachis jointed, with the spikelets firmly fastened to the joints, while the domesticated wheat has the rachis entire and the spikelets jointed to the rachis.

The jointed rachis is not the only difference in the structure of the head of the wild wheat. Instead of dropping apart and allowing the grains to fall out at maturity, the spikelets of the wild wheat function as useful organs for disseminating and planting the seeds. The glumes are very hard and tough and are grown fast to the joints of the rachis. Instead of being readily broken off and separated from each other to liberate the kernels, as in the domesticated wheat, the kernels of the wild wheat are not normally released from the spikelet. A simple rubbing in the hand is sufficient to separate the glumes and kernels of the domesticated wheat from each other and from the rachis, but much more persistent rubbing leaves the spikelets of the wild wheat still intact. Indeed, it is very doubtful whether the wild wheat could be thrashed with any ordinary machinery, so compact and tough are the spikelets.

THE SPIKELETS AS BURROWING ORGANS.

The highly specialized nature of these joints of the rachis may also be judged by the fact that the articulation is not at the end, but on one side. The effect of this adaptation is to leave the end of the beak nicely smoothed and rounded, well suited for slipping along over ordinary surfaces, not pointed enough to enter or be impeded by minute apertures or roughness, but well suited to creep into larger crevices under stones and clods or to burrow into loose earth.

In an open space without obstructions the spikelets could be blown long distances or they could be lifted by whirlwinds, which must be effective agents of dissemination of plants in desert regions. But even under ordinary conditions, in the presence of many plants and the surface inequalities of rocky soils, the wild-wheat spikelets are probably able to creep along for several feet. This was indicated by the many cases in which numerous spikelets were found crowded

under the same stone or deeply buried in the same little mound of loose earth thrown up by moles or burrowing rodents.

The spikelets evidently do not cease their movements as soon as shelter is found, but often continue to burrow until only an inch or less of the ends of the beards remains exposed. Further appreciation of the burrowing mechanism is gained when an attempt is made to draw the spikelets out of their retreats. A strong pull is likely to be required unless the earth happens to be loose. Many attempts fail because the tough beards often break off, leaving the buried spikelets behind. That the spikelets can be so deeply buried by the action of the wind alone is hard to believe. Hygroscopic movements are possible, such as the twisting and untwisting of the beards by daily changes of humidity.

RELATION OF DISSEMINATION TO CROSSING.

Specializations that assist in the dissemination of seeds serve not only to extend the geographical distribution of the species, but probably have a still more important physiological function in facilitating cross-fertilization. If the seeds have means of being carried about, the plants of the next generation are much less likely to have close relatives as neighbors. A wider range of cross-fertilization is secured, which contributes to the vigor and fertility of the species.

From this point of view it is possible to appreciate another reason for the evident tendency to reduce the wild-wheat spikelets to a single fertile seed. The development of two seeds from the same spikelet may involve not only an undesirable competition between the two plants but a mutual injury from consanguineous pollen. Thus, it is possible to understand how the development of an indehiscent spikelet for the better protection, dissemination, and planting of the seeds would establish in turn a condition of natural selection in favor of the reduction of the spikelet to a single fertile seed.

INEQUALITY OF SEEDS.

The extent to which spikelets of the wild wheat represent specialized organs for planting the seeds may also be judged from another curious fact shown in an experimental planting of the wild wheat at San Antonio, Tex., in the spring of 1911. Although two seeds are present in most of the spikelets, it is unusual for more than one of them to germinate. Out of 175 spikelets dug up at San Antonio only 6 showed the development of two seedlings from the same spikelet. A detailed examination showed 31 single-seeded spikelets, leaving a remainder of 138 with two seeds in each spikelet, only one of

which germinated. The two seedlings that were produced from the same spikelets in the six cases were approximately equal in size, and like those from the other spikelets, they were already several inches tall. None of the second seeds in the other spikelets showed any sign of germination. In a few instances decay had set in, but most of the seeds were still intact. The endosperm was softened to a pasty consistency, though still pure white. This seemed to exclude the possibility that failure to germinate had been due to lack of moisture.

An examination of a sample from the same stock of imported seed from El Hadr, Palestine, showed 144 spikelets with two seeds to 93 with one seed. The large and small kernels were sorted apart as the spikelets were opened and weighed separately. The average weight of the 144 large kernels was 0.027 gram, while the small kernels weighed only 0.018 gram. The 93 kernels from the single-seeded spikelets gave an average of 0.022 gram, which figure also represented the general average for the total number of 381 kernels.

The nature of this specialization is not yet apparent. At least three possibilities have to be considered. One of the seeds may be imperfect and unable to germinate or the germination of one seed may in some unknown manner prevent the germination of the other. Again, the seeds may be unlike, so as to germinate at different times, in some such way as in Atriplex and Xanthium. Some of these possibilities are easily tested, but others may require some time.

Whatever the nature of the specialization, its advantage is plain. It is easy to understand that in dry regions like those where the wild wheat is native the germination of a single seed is much more likely to be accomplished safely than that of two seeds. And even after germination the chances of reaching a productive maturity would be much greater for one plant standing alone than for two plants standing close together and competing for the scanty moisture of the soil.

POSITIONAL RELATIONS OF SEEDS AND GLUMES.

When the awns are distinctly unequal, as they usually are, it is always the basal flower that has the larger awn and the second flower that has the smaller. The smaller awn always accompanies the glume that projects the most at base, unless it is very much reduced. On the other hand, it is the basal flower that has the smaller grain.

The possibility that the inequalities of the awns and seeds might have some relation to their position on the head was considered, but no consistent differences were noticed. As the heads stand in oblique positions, the spikelets are not regularly arranged to have the large awn above or below, nor is there any regular alternation. On some heads several spikelets that show the same position of the

large and small awns may be found on the same side, followed by an abrupt change to the other kind of spikelet.

If the spikelets are laid down in the same position, some will appear to be right handed and others left handed, with reference to the large awns. This relation is determined by their position in the spikelet, but seems to have no regular relation to the position of the spikelet on the head. It seems to be entirely a matter of chance whether a spikelet is to be right handed or left handed. This is indicated by equality in the numbers of right-handed and left-handed spikelets. A count of 224 spikelets showed 112 right handed and 112 left handed.

The presence of more heavy grains on one side may affect the position of the heads, which often stand in inclined or oblique positions with the broad sides of the heads facing upward and downward. In the usual positions of the heads of the wild wheat the rachis stands on edge, which is at right angles with the position of inclined heads of domesticated wheat where the rachis lies on its side, with one row of spikelets above and the other below.

RELATIONSHIPS OF THE WILD WHEAT.

The relationships of the wild wheat are of practical interest from the standpoint of breeding, quite apart from the question of a direct utilization of the plant. In the investigation of breeding problems, there is a distinct advantage in having two or more allied plants to serve as a basis for comparison. Many variations and differences of behavior that would otherwise escape notice are likely to be brought out by comparison. Even the most familiar facts may fail of proper appreciation until they are thrown into contrast by comparison with different characters or conditions. Though the comparative methods have been generally recognized as the chief basis of modern biological science, the application of such methods is frequently neglected in dealing with practical problems. In attempting to determine the direct economic value of a plant it is easy to overlook the indirect economic value that it may have in throwing light upon the behavior of another species.

HISTORICAL INTEREST OF THE WILD PROTOTYPE.

In addition to the interest of the wild wheat from the breeding standpoint is its historical interest as a possible prototype of the most important of cereals. To locate the original home and place of domestication of the wheat plant is also to locate a probable center or starting point of ancient civilization.

This preeminent interest of the wheat plant may be questioned, perhaps, on the ground that the rice plant of tropical Asia or the maize

plant of tropical America sustains more millions of people or represents a more ancient domestication than the wheat plant. Yet the wheat was at least the chief basis of the ancient civilization of the Mediterranean region, as well as of the modern civilization of northern Europe, to say nothing of the Asiatic countries where wheat was grown in ancient times or of the more remote regions in America and Australia that have been occupied in recent centuries by wheat-growing European populations.

That Palestine has a wild wheat plant, with all the characters predicted for the unknown prototype by the most eminent European specialists, Mr. Aaronsohn has certainly demonstrated, but a number of problems remain to be solved by further explorations and experiments before the prototype question can be said to have had an adequate scientific treatment. Some of these inquiries are already receiving Mr. Aaronsohn's attention, and additional evidence may be expected at any time.

THE JOINTED RACHIS A PRIMITIVE CHARACTER.

The jointed rachis, which has been so largely relied upon as a distinguishing feature of a true prototype, is hardly to be considered sufficient ground for a final determination. That some more or less remote ancestor of the domesticated wheat had a jointed rachis is not an unreasonable assumption in view of the agreement in this respect among many wild species of several related genera of grasses—Triticum, Hordeum, Agropyron, Aegilops, etc. Even the presence of long beards in domesticated wheats may be used as an indication of an originally jointed rachis, since it is only in connection with such a rachis that beards appear to have a definite function in planting the spikelet. But these deductions throw no light on the question whether the function was lost before domestication took place or afterwards. The beard and rachis characters are present in many wild grasses and absent in many others.

Something may be learned regarding the rachis characters by the study of hybrids, some of which have been already made in Germany by the younger Koernicke and in Palestine by Mr. Aaronsohn. It may be that the analogy of hybrids between wild and domesticated types of barley, studied by Koernicke and Tschermak, will also apply to wheat. These investigators found that the brittle rachis of the wild barley did not behave as a dominant character, but disappeared in the hybrids. This is also true of the supposed natural hybrid between the wild wheat and *Aegilops ovata*. The three spikelets that formed at least the upper part of the head are firmly joined together, as in Aegilops, instead of being the first to fall apart, as in the wild wheat.

The analogy in some of the characters seems very close between the wild wheat and the emmers, but even though the wild wheat be accepted as the prototype of the emmers there is still a question as to whether the emmers came from the same original domestication as did the true wheats. In view of the rich diversity of forms in the genus Triticum and its relatives there is nothing unreasonable in the idea that several wild species were domesticated, as most botanists seem to have concluded in proposing and accepting the current classifications.

The general occurrence of wild wheat with wild barley has suggested to Mr. Aaronsohn the probability that the two might have been domesticated together. But if cereals as diverse as wheat and barley were not distinguished by primitive man there is less reason to believe that a separation would be made between the different kinds of wheat or between wheat, spelt, and emmer. The same general tendencies of unconscious selection, to suppress the jointed rachis and the cross-fertilizing adaptations, are apparent in barley and oats, as well as in the different kinds of wheat. Even if the different forms of Triticum did not grow in the same localities originally, such mixtures might easily be made with the extension of cultivation into other regions, just as the corn cockle, chess, and other weeds have been spread with wheat. For primitive peoples a mixture of several cereals might be better than a pure stock, for the crop might be safer, even if less abundant. The custom of planting mixed grains seems to have continued in Europe nearly to the present day. The combination of wheat and rye even had a special name in English and in French, "meslin" and "méteil," respectively.[1]

POSSIBLE EXISTENCE OF OTHER PROTOTYPES.

The botanical evidence may be sufficient to show that the jointed rachis is a primitive character for a large group of species, but this affords no assurance that any particular species with the jointed rachis was the long-sought prototype of wheat. That so common and even so conspicuous a grass as wild wheat should remain so long overlooked in a country that has received as much botanical attention as Palestine, makes it entirely conceivable, to say the least, that other wild species of Triticum may exist in the Arabian Peninsula or

[1] "Meslin, or méteil.—The French have a custom of cultivating what they call méteil, but what is called, in English, meslin; that is, a mixture of wheat and rye. The proportions are not very exactly determined. If the land is more favorable to wheat than rye, more of wheat is sown in the mixture than of rye, and the contrary. It yields a good crop when sown after wheat, when wheat following wheat would not be advisable. This culture is far from being universally approved in France; but some eminent farmers maintain that the crop is more sure than any other, that it is not easily lodged, and that neither the rye nor the wheat is so liable to rust or mildew as when cultivated alone. It sometimes happens, likewise, that the season is not favorable to one of the kinds of grain when the other yields a crop. It follows potatoes to advantage. It is generally consumed on the farm in preference to being sent to market, and it makes a healthy bread." (Colman, Henry, "The Agriculture and Rural Economy of France, Belgium, Holland, and Switzerland," 1848, p. 163.)

in the other vast regions of western and central Asia, which have not received a tithe of the botanical attention given to Palestine.

And even though no other wild types of wheat should be discovered by further exploration, there is another interesting possibility in more definitely fixing the status of the domesticated type of wheat, which grows so frequently as a spontaneous plant. That it is not a wild plant in Palestine, at least in any such sense as the wild wheat, is very apparent in the districts where the wild wheat grows, and may be true of all the adjacent regions, as Mr. Aaronsohn's observations have led him to conclude, but if the domesticated type of wheat could be found to behave as a wild plant in Arabia or elsewhere in western Asia there might be no necessity of looking to any different plant as a prototype.

As pointed out by Mr. Aaronsohn, the wild wheat seems to be rather strictly confined to the calcareous soils in the region of Mount Hermon, and is often completely absent from the small areas of volcanic soils that in many places interrupt the limestone formations. Whether this apparent preference for limestone has reference to chemical or to physical factors is not yet known. The volcanic soils, though often very fertile, may remain too dry at the surface to permit the germination of the seedlings. On the other hand, the spontaneous or escaped form of domesticated wheat often seemed to prefer volcanic soils. This was noticed especially in the vicinity of El Hadr, where the spontaneous wheat was sometimes abundant, even in places that did not seem to have had any recent cultivation, though the seeds may have been dropped from the harvests of neighboring fields.

TRITICUM MONOCOCCUM EXCLUDED AS PROTOTYPE.

That another wild wheat should exist in the same region, though in a different geological formation, would not be an argument against the possibility that the spontaneous wheat of the volcanic soils might represent the ancestral form of the domesticated type. Indeed, the Palestine country affords three spontaneous types of Triticum, for Mr. Aaronsohn has found a wild form of *T. monococcum,* only very slightly different from the cultivated einkorn. This species is not known to be cultivated in Palestine or adjacent regions, though still grown to a slight extent in Europe. At the time of Schliemann's excavations of the site of ancient Troy it was reported that the einkorn wheat had been found, which suggested the idea that the einkorn might represent the primitive form of cultivated wheat, but Mr. Aaronsohn states that Wittmack afterwards identified the specimens as barley, on the basis of a microscopical examination. Another reason for excluding *T. monococcum* from consideration as a possible

prototype of domesticated wheat is the fact that it has not been found to produce fertile hybrids with the other cultivated species of Triticum.

Spelt also has been looked upon as a primitive type of wheat, but it seems not to have been mentioned before the time of the Emperor Diocletian. Thus, by a process of exclusion it has been argued that emmer (*Triticum dicoccum*) must represent the most primitive type, so that Mr. Aaronsohn's wild emmerlike plant certainly leaves nothing to be desired from the standpoint of the theories of the German specialists. On the basis of the existing knowledge of the plants and their habits the only other alternative that seems worthy of consideration is the possibility that the cultivated wheat represents its own wild prototype more nearly than the other plants that have been proposed as ancestors.

SPONTANEOUS FORMS OF DOMESTICATED WHEAT.

In other words it is a choice between the wild wheat of Palestine and the plant that has been looked upon as an escaped or spontaneous form of the domesticated wheat. Acceptance of the latter alternative would bring the wheat plant directly into line with what is known regarding the wild types of other agricultural plants of Old World origin. It seems to be a general fact that the domesticated plants of the Old World are still very closely similar to their wild ancestors, whereas in America several of the most important domesticated plants, such as Indian corn, coconuts, cassava, and peanuts have not been found to represent any wild species now in existence.

So far as the jointed rachis bears on the question it does not seem any less reasonable to consider the possibility of finding a wild wheat without a continuous rachis or less specialized joints than to believe in the development of the domesticated type of wheat from a plant with the rachis so highly specialized as the wild wheat of Palestine.

COMPARISON OF WILD WHEAT WITH AEGILOPS.

As an example of the suppression of the joints of the rachis in a wild relative of wheat, mention may be made of *Aegilops ovata*, a plant very common in the wild-wheat country of Palestine, formerly considered as the prototype of wheat by De Candolle and others. In this species of Aegilops, specialization has taken the direction of uniting some of the joints of the rachis, so that the whole head functions together as an organ of dissemination. The head is articulated only at the base, below the fertile spikelets, of which there are usually two. The second fertile spikelet is permanently attached to the first, as well as the reduced sterile spikelets that form a stiff brush of bristles. The suppression of articulations in this wild plant makes

it unnecessary to suppose that the continuous rachis of the domesticated wheat has been derived in domestication, or that the jointed rachis is a necessary character for all wild types.

If the wild prototype of the wheat had a jointed rachis, it is strange that reversions to this condition should not occur, at least in small depauperate forms of the domesticated species; yet no such tendency was noted in any of the spontaneous wheat in Palestine.

ORDER OF MATURITY OF SPIKELETS.

According to Mr. Aaronsohn's observations, the order of maturity of the spikelets on heads of domesticated wheat is not the same as on the wild wheat. As might be expected from the earlier maturity of the seed, the terminal spikelets of the wild wheat are the first to develop their flowers, whereas in the domesticated type the spikelets near the middle of the head are the first to mature. While such a change of the sequence of maturity of the flowers appears much less serious than the modifications that must be assumed to have taken place in the structure of the rachis, the fact can hardly be considered as an evidence of close relationship. There is no apparent reason why a loss of the structural specialization of the rachis should have involved a change in the order of the development of the flowers.

Another feature in which the wild wheat seems more specialized than the domesticated type is the greater reduction of the middle or infertile flower of the spikelet. In some varieties of wheat the spikelets have several fertile flowers. A single smutted head of domesticated wheat found at El Hadr had an increased number of seeds in the spikelets.

SEEDLING CHARACTERS OF WILD WHEAT.

Although the spikelets of Aegilops are very different from those of Triticum, Ascherson has united the genera because *Aegilops ovata* has been found to hybridize readily with wheats and has three radicles instead of one, as in other species of Aegilops. Triticum has three radicles and Secale four.

Germinating seedlings of the wild wheat are not absolutely regular in the number of radicles; most of them put forth three, though in some cases there are only two, and occasionally four or five. A count of the radicles of some seedlings of wild wheat germinated at San Antonio, Tex., in April, 1911, showed 162 with three radicles, 12 with two radicles, 4 with four radicles, and 2 with five radicles.

Unlike the wild barley, the radicles of the wild wheat emerge from both faces of the spikelet. In the barley the whole group of five or six radicles breaks through the outer face of the spikelet. The

scutellum of barley lies parallel to the outer face of the spikelet, while that of the wheat lies across the spikelet. Though the emergence of the radicles of the wild wheat from both faces of the spikelet is a constant feature, there is no apparent regularity in their distribution. Of 150 spikelets where this point was noted, two of the radicles came from the outer rounded face of the spikelet in 80 cases, while two came from the inner face in 70 cases.

WILD WHEAT AND WILD BARLEY.

It is not easy to believe that a plant so highly specialized as the wild wheat of Palestine should have lost so many of its peculiarities as the cultivated types must be supposed to have done, if the wild wheat is to be accepted as the true prototype. The domesticated barley seems much closer to the wild species than in the case of the wheat, not only in the structure of the rachis, but in that of the spikelet as well. The 6-rowed barleys represent the loss of one of the specializations of the wild type, the reduction to a single fertile spikelet, but the 2-rowed types of barley offer very close and very general analogy with the wild plant. Some writers have held that the 6-rowed barley must have been derived from a different wild species. Some of the wild species of Hordeum in Palestine have the seeds arranged in 6 rows, with a superficial resemblance to the 6-rowed barley.[1] The loss of the jointed rachis in the domesticated barley renders the beards as useless, as organs of dissemination, as those of the domesticated wheat. Nature abounds in examples of apparently useless characters, but it is difficult to believe that so specialized an organ would have developed unless it had adaptive value for the wild ancestral type.

SELECTIVE ELIMINATION OF CROSS-FERTILIZATION.

The cross-fertilizing adaptations in the wild wheat do not constitute an objection to its being considered as the true prototype. Not only are such adaptations shared to some extent by the domesticated species, but the conditions of domestication involve an important factor of unconscious selection toward the habit of self-fertilization. With the wheat growing as a wild plant under ideal weather conditions, like those found on the slopes of Mount Hermon in May and June, natural crossing is on the same footing as in other wild plants of similar habits.

As soon as such a plant began to be grown as a cultivated crop and extended to more extreme conditions, unconscious selection

[1] Mr. Aaronsohn states that he has crossed the 2-rowed wild barley (*Hordeum spontaneum*) with domesticated 4-rowed barley and that a considerable number of 6-rowed ears appeared in the first generation, though most of the ears were of the 4-rowed form.

would favor self-fertilization. In proportion as the weather is too dry or too wet or too cold for cross-fertilization at the time of flowering, the resulting crop is limited to the lines of descent that have the habit of self-fertilization. The exsertion of the anthers and the opening of the glumes would be ineffective or even injurious in bad weather. Lines of descent dependent upon cross-fertilization would be eliminated. Eventually only those lines would remain that brought the stamens and stigmas to maturity at the same time. All tendencies toward dimorphic conditions of proterandry or proterogyny would be forbidden by unconscious selection. The same result has been reached in some of the carefully bred varieties of corn, though all of the more primitive types show a pronounced condition of proterandry.

CONDITIONS OF DOMESTICATION OF WILD WHEAT.

DIFFICULTIES OF PRIMARY DOMESTICATION.

Another point of view from which the prototype question may be approached is that of domestication. Is such a plant as the wild wheat likely to have been domesticated by primitive man or is it more reasonable to believe that the true prototype must have been better suited to domestication? Or it may be asked whether the domestication of such a plant as the wild wheat could have represented a new or independent beginning of the art of agriculture. The alternative possibility is that instead of such a direct or primary domestication there may have been an indirect or secondary domestication by a people with agricultural habits already established.

Considering the plant alone, apart from any historical prepossessions, it must be admitted that the jointed rachis, long beards, and tough, close-fitting glumes would render the wild wheat a rather unpromising subject for domestication at the hands of a very primitive people. The seed is hard to collect and hard to separate from the chaff. Though the plants grow abundantly in some localities, the difficulties of collecting the grain and separating it from the chaff would stand in the way of its becoming the sustenance of a very primitive nonagricultural people or of serving as the basis of an original development of the art of agriculture.

Without an equipment of baskets or bags for gathering the separate spikes or a habit of using mortars or other means of beating out and winnowing the grains, the utilization of such a plant would seem well-nigh impossible. The traditional method of cutting or pulling the heads of wheat and binding them into bundles could not be applied at all to the wild wheat because of the jointed rachis, which allows the spikelets to fall apart as soon as they are mature. Ordi-

nary treading or thrashing would be quite ineffective for separating the wild-wheat grains from the chaff of the firmly closed spikelets. With the beards and bristles burned off and the chaff made brittle by exposure to fire and then beaten in a mortar, a separation of the grains could probably be accomplished.

Attention has been called by Mr. F. H. Chittenden, of the Bureau of Entomology, to the unusual hardness of the grains of the wild wheat as likely to give it protection against insect injury in storage, though in a few cases the husks of the imported seed showed signs of attack by the Angoumois grain moth (*Sitotroga cerealella*), a well-known cosmopolitan insect which preys upon practically all cereals. The hardness of the grains would not interfere with domestication by a people accustomed to soften their food by soaking, grinding, or cooking, but would offer some difficulties under the theory that primitive man began by eating raw cereals.

SECONDARY DOMESTICATION MORE PROBABLE.

When the wild wheat is able to invade cultivated land it grows much more vigorously and forms larger and more numerous heads in a way that would be much more likely to secure the attention of a primitive people. It is conceivable that an agricultural tribe settled in a neighborhood where the wild wheat grew might gather the grain in times of scarcity and finally adopt the plant into cultivation. It is possible that the plant grew wild in former times in the more favorable places that are now under regular cultivation. But any considerable extension of this kind may be doubted, in view of the probability that permanent vegetation of shrubs and trees formerly occupied all except the most rocky and barren lands, where the plant still seems to find its most congenial home. Instead of agriculture having restricted the distribution of the wild wheat, the denudation of a country like Palestine is much more likely to increase the distribution of the desert types, which gradually replace those that require fertile or moist soils.

Assuming that the wild wheat is the true prototype of our cultivated wheats, it would seem most reasonable to believe that the domesticators of such a plant were already an agricultural people accustomed to the use of other seed plants for food and equipped with some primitive means of gathering and thrashing, as well as of grinding and cooking. In Mexico and other parts of tropical America wild seeds are often gathered by agricultural Indians to supplement corn or other crops. Among the California Indians the arts of gathering, winnowing, and grinding wild seeds were highly developed. This was true even in tribes that had no agriculture at all, though such habits might have been borrowed from the agricultural tribes

in the southern part of the State. Moreover, the California seed-eating Indians had settled habitations or, at least, were confined to limited districts, instead of being pastoral nomads, as the early inhabitants of Palestine are supposed to have been.

BORROWING OF DOMESTICATED ANIMALS AND PLANTS.

The treatment of wheat and other small grains as secondary domestications is in line with the probabilities regarding the domestication of animals. Instead of taking it for granted that the pastoral state was antecedent to agriculture, it should be recognized that settled agricultural tribes are much more likely to domesticate animals than are wandering savages, who live by hunting or fishing. The domestication of many species of animals in the Old World also presupposes the existence of a settled agricultural population. After animals have been domesticated they may be adopted by wandering hunting tribes that come into contact with more advanced agricultural peoples.

Many of our western hunting Indians, who long ago adopted horses and other domestic animals from the white man, still have very little interest in agricultural plants. But among the Indians of tropical America, where agriculture appears to have originated, many plants were found in cultivation by people who had no domestic animals at all or only household kinds, like parrots, guinea pigs, and dogs. With the exception of the llama of the mountains of Peru, no large grazing animals seem to have been domesticated in ancient America. There was nothing to compare to the horses, asses, camels, elephants, cattle, buffaloes, goats, sheep, pigs, etc., that were domesticated by the agricultural populations of the Eastern Hemisphere. Yet it is not to be imagined that the domestication of animals in the Old World preceded the domestication of plants any more than in America. Though the adoption of domestic animals may represent the first stage in the borrowing of an agricultural civilization, the original taming and domestication of an animal implies a settled existence and an adequate supply of food for the men themselves as well as for the animals; in other words, an agricultural status.

CIVILIZATION NOT INDIGENOUS IN EGYPT OR MESOPOTAMIA.

Modern archæological discoveries in Egypt and Mesopotamia tend to discredit the traditional idea that those regions were the scene of the first development of agriculture. The earliest civilizations in both countries are now ascribed to foreign populations that came in from the Indian Ocean or southern Arabia to Mesopotamia by way of the Persian Gulf and to Upper Egypt from the Red Sea. It was

formerly supposed that civilization was established earlier in the delta region of Egypt because of its proximity to Asia, the traditional home of the human race. It is now known that the civilization of Upper Egypt was more ancient than that of Lower Egypt and that the conquering race that established the historical dynasties came in from the East. Similarities are still recognized between the early stages of civilization in Egypt and those of the Chaldeans and Sumerians at the head of the Persian Gulf, but the present tendency is to explain these primitive approximations by community of origin from southern Arabia rather than by subsequent borrowing.

Notwithstanding the great antiquity of Egyptian civilization, it does not appear that the natural conditions in that country could have been very favorable for a first beginning of the art of agriculture. According to Herodotus the Egyptians had traditions of a time when all of the lower part of Egypt was a mere swamp, unfit for human habitation. The country must have been originally a flood plain of the Nile, with the native vegetation limited to plants that could endure the annual alternations of deep flood and prolonged drought, conditions that must have been unfavorable to the existence of wheat or other cultivated plants in a wild state. The native flora of Egypt may have been something like that of the flood plains of our southwestern rivers. The common Egyptian acacia recalls the screw bean and mesquite of the lower valley of the Colorado River in Arizona and California, a region capable, like Egypt, of supporting a large civilized population, but occupied hitherto by only a few scattering communities of very primitive Indians. Though it is now known that there was a native prehistoric population in Egypt before the dynastic invaders arrived, it is not certain that the native race occupied the actual flood plain of the Nile Valley to any such extent as in later and more civilized times. The stone implements and other characteristic remains of the primitive people have been found chiefly along the borders of the desert and in the Fayum and other oases rather than in the flood plain or Nile Valley proper.

ANTIQUITY OF AGRICULTURE IN AMERICA.

The tracing of the Egyptian and Chaldean civilizations, supposedly the most ancient, to southern Arabia has naturally suggested the possibility of a relation between the primitive civilization of Arabia and that of the shores of the Indian and Pacific Oceans. The same primitive system of tropical agriculture, accompanied by the same Polynesian type of language, extends all the way from Madagascar across the Malay region and all the inhabited islands of the Pacific Ocean. Moreover, the coconut palm and several other domesticated plants widely distributed in the Old World Tropics in

prehistoric times appear to have been of American origin, which would indicate that there was a Trans-Pacific communication of agricultural plants in early prehistoric times. That the agriculture of tropical America is more ancient than that of Asia or Africa is also indicated by the fact that the plants domesticated in the Eastern Hemisphere are still very similar to their wild relatives, whereas it has been very difficult to settle upon the wild types of many of the agricultural plants of America.[1]

Though all the natives of America are considered by ethnologists as belonging to one general racial type, the local specializations of physical features, language, agriculture, and other arts and customs are such as to indicate a slow and gradual development through a very long period of time. The recent archæological discoveries in Egypt and Mesopotamia indicate that agricultural civilization may have existed in the Old World for 10,000 or 20,000 years. The archæological evidence regarding the antiquity of civilization in America is less direct, but from ethnological, biological, and agricultural considerations it seems not unreasonable to believe that the development of agriculture in America covers a much longer period than in the Old World, perhaps five or ten times as long.[2]

DIVERSITY IN WILD AND DOMESTICATED WHEATS.

INDIVIDUAL AND LOCAL DIFFERENCES IN WILD WHEAT.

Attention has been called in Mr. Aaronsohn's bulletin to the wide range of variation shown by the wild wheat. As such variations promised to be of interest from the standpoint of acclimatization it was intended to give them special attention in the field, in order to learn whether they represented local varieties or subspecies or only the normal individual diversity (heterism) of wild species. The heads of individual plants were to be collected separately as material for subsequent study and illustration of the facts of diversity.

It was soon found that the habits of the plants stood seriously in the way of securing definite results by this method. Plants that grew in uncultivated land generally produced only one or two heads and these often small, so that only a few seeds could be obtained from such individuals. Plants that had found more favorable conditions in cultivated fields often produced 10 or 15 heads as a result of abundant stooling, but it was seldom possible to determine with certainty that the whole cluster had come from a single original seed.

[1] Cook, O. F. Food plants of ancient America. Annual Report, Smithsonian Institution, 1903, p. 481-497. See also "History of the coconut palm in America," Contributions from the U. S. National Herbarium, vol. 14, p. 271, 1910.

[2] Cook, O. F. Vegetation affected by agriculture in Central America. Bulletin 145, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

In order to be certain that all of the heads from such clusters represented the same individual plant it would be necessary to locate and mark the individuals in the early stages of growth, before stooling began, or, better yet, to raise the plants from seed under experimental conditions. In view of these limitations it seemed best to spend the short time available in more general observations of the habits and characters of the plants and leave the more detailed study of the individual differences until some better opportunity could be secured.

Regarding the general question of the nature of the differences it became obvious enough that at least three factors or forms of diversity, which may be described as environmental, individual, and local, had to be taken into account. In addition to the differences of behavior that could be ascribed to inequalities of soil, moisture, or temperature, many individual differences of color, hairiness, pruinescence, and other details were always to be found among the plants of each locality where such comparisons were made. Perhaps the most obvious structural differences are those resulting from the varying development of the teeth at the outer angles of the glumes. A series of eight pairs of glumes taken at random from a stock of imported seed of the wild wheat collected at El Hadr is shown in figure 3.

FIG. 3.—Glumes of wild wheat, showing variations in the teeth. (Natural size.)

There were also more general differences that served to characterize local forms or races. Thus, in a nummulitic limestone district between Rosh Pinar and Khan Jubb Yusef, all of the wild wheat seemed to have the outer glumes of the spikelets densely hairy, much more so than in any of the plants previously studied on the slopes and foothills of Mount Hermon. (See Pls. VIII and IX.) A few miles nearer the Lake of Gennesaret (Bahr Tabariyeh) another form of wild wheat appeared, with the glumes smooth, but of very large size. Spikelets with hairy glumes occurred also at the same place, but were not so strongly hairy as in the previous locality.

The individual diversities were much more apparent among the large, many-headed plants in cultivated land. This may be ascribed in part to the fact that the large plants give much better opportunities

for observation. The repetition of the same characteristic by several large heads of the same plant brings them much more effectively to the observer's attention than if they are shown in only one or two small heads.

CORRESPONDING DIFFERENCES IN DOMESTICATED WHEAT.

Equally apparent differences in the extent of individual diversity under different conditions was also noticed in the domesticated type of wheat. The spontaneous plants usually produced only a single small head and seemed to show only about the same amount of diversity as the wild wheat. The color differences appeared somewhat less pronounced in the spontaneous plants of the domesticated wheat, but in the arrangement of the spikelets on the heads and the amount of bloom on the surfaces the escaped wheat appeared to be somewhat more variable than the wild type. Even in different fields of cultivated wheat there seemed to be distinct differences in the extent of diversity among the plants. On the higher slopes of Mount Hermon and in other places where the conditions were unfavorable, so that the plants remained small, they seemed much more alike than in the more fertile fields that had produced well-grown plants. Indeed, Palestine can still boast of many magnificent wheat fields in spite of age-long cultivation; nor has any attempt at selective improvement shorn away the primitive diversity of the cultivated plant, which even exceeds that of the wild type.

The great differences in the shape of the heads are responsible, no doubt, for the more obvious diversity of the domesticated wheat. In addition to a full series of different forms of heads, clubbed and open, broad and narrow, square and flat, there is an equally complete range in color—white, black, and red. Some heads are beardless, some have short beards, and some very long. The surfaces of the glumes are smooth or velvety, pruinose or naked, and so on through the whole series of details that are used to distinguish selected types of wheat.

NATURE AND SIGNIFICANCE OF DIVERSITY.

From the standpoint of some theories of heredity these displays of diversity in both the wild and cultivated types of wheat could not be supposed to have any biological interest or practical significance. They would both be looked upon as ordinary examples of what might be found in the field of almost any careless farmer in the United States—a mixture of different varieties. (See Pl. X.) When the facts are more carefully considered, this interpretation proves inadequate. It is certainly unreasonable to believe that anybody has ever separated the wild wheat into uniform varieties and then mixed them together again, nor is such a theory more justified in connection with the cultivated wheat of Palestine.

The nature and extent of the diversity in the domesticated type of wheat in Palestine may be judged by reference to Plate XI, which represents a few casually selected ears from the same field. In one case, at El Hadr, an attempt was made to find additional ears of a deep red, compact-headed form that happened to attract attention.

Figure 4 shows six ears that were picked as possible representatives of the desired type. Comparison showed, however, that they differ among themselves almost as much as the rest. One of the heads has black beards and very long beardlike teeth on the outer glumes. One of the other heads is heavily pruinose, while in another the glumes are nearly smooth and distinctly lighter in color, etc. Closer approxi-

FIG. 4.—Heads of domesticated wheat from El Hadr, Palestine, selected to show similarity of form and color. (Natural size.)

mations of type could doubtless be found by more careful comparison in the field, but before such selection can be undertaken to the best advantage something should be known regarding the adaptive values of the different characters and combinations.

The supposition of a previous selection of the domesticated wheat appears the more improbable when applied to such primitive people as the Druse mountaineers, who are the wheat growers of the slopes of Mount Hermon. That higher civilizations existed in these regions in ancient times than at the present may be true, but there is nothing to indicate that the primitive farming population of the Druse Mountains ever carried the selection of wheat any farther than at present.

In this respect, at least, it is reasonable to suppose that present conditions have existed from immemorial times. Damascus, on the plain to the east of Mount Hermon, has the traditional distinction of being the oldest city in the world.[1]

SELECTION OF UNIFORM TYPES A MODERN ART.

De Vries infers that pure races of cereals were known to the Romans and quotes some lines from Vergil's Georgics in proof of the assertion. The passage states that the largest ears must be selected every year if degeneration is to be avoided, but this seems very far from the idea of isolating pure races. If such a degree of agricultural advancement had been attained among the ancients it is strange that no more definite reflections of it should have survived in literature. Even among the Chinese, who practiced conscious selection for many centuries, the idea of separating pure races of annual-crop plants seems not to have developed. In modern Europe this idea appears to be only about a century old, even if dated back to Lagasca's suggestion to Le Couteur, though that seems to have contemplated the classification of a diverse stock into types rather than a separation of progenies of single individuals as parents of pure races.[2]

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[1] The Druses are a hardy agricultural people, physically well favored, and industrious. Their religion is said to forbid the use of narcotics in any form, including tobacco. Even coffee is refused by some, though used by our entertainers at El Hadr, flavored with seeds of Moringa. The Druses are said to have traditions of an emigration from Yemen in the seventh century, but such traditions are likely to refer to a noted warrior or band of conquerors who settled in the country, and would not preclude the possibility that the present population is essentially indigenous. The people are certainly entirely distinct both in features and habits from the surrounding desert Arabs, as well as from the Jews.

[2] De Vries describes this event as though the idea of separating the components of a mixed stock were entirely new:

"The fact that our cultivated plants are commonly mixtures of different sorts has not always been known. The first to recognize it seems to have been the Spanish professor of botany, Mariano Lagasca, who published a number of Spanish papers dealing with useful plants and botanical subjects between 1810 and 1830, among them a catalogue of plants cultivated in the Madrid Botanical Garden. Once when he was on a visit to Col. Le Couteur on his farm in Jersey, one of the Channnel Islands off the coast of France, in discussing the value of the fields of wheat, he pointed out to his host that they were not really pure and uniform, as was thought at that time, and suggested the idea that some of the constituents might form a larger part in the harvest than others. In a single field he succeeded in distinguishing no less than 23 varieties, all growing together. Col. Le Couteur took the hint and saved the seeds of a single plant of each supposed variety separately. These he cultivated and multiplied till he got large lots of each and could compare their value. From among them he then chose the variety producing the greatest amount of the finest, whitest, and most nutritious flour. This he eventually placed in the market under the name of 'Talavera de Bellevue.' It is a tall, white variety, with long and slender white heads, almost without awns, and with fine, white, pointed kernels. It was introduced into commerce about 1830 and is still one of the most generally cultivated French wheats. * * * Hallet, the celebrated English wheat breeder, tried in vain to improve the peculiar qualities of this valuable production of Le Couteur's." (De Vries, "Species and Varieties, Their Origin by Mutation," 1905, p. 96.)

The first instance of isolation of the progeny of a single plant reported by De Vries was that of the Scotch breeder Sheriff in 1819. De Vries states:

"In the spring of 1819 he observed quite accidentally in a field of the farm of that name [Mungoswell] a single plant which attracted his attention by a deeper green and by being more heavily headed out. Without going into further details, he at once chose this specimen as the starting point of a new race. He destroyed the surrounding plants so as to give it more space, applied manure to its roots, and tended it with special care. It yielded 63 heads and nearly 2,500 grains. All of these were sown the following fall, and likewise in the succeeding years the whole harvest was sown in separate lots. After two years of rapid multiplication it proved to be a good, new variety and was brought into commerce." (De Vries, "Species and Varieties, Their Origin by Mutation," p. 110.)

Neither the diversity of the wild wheat nor that of the stock cultivated by the primitive people of Mount Hermon is to be considered as a peculiar or unusual fact demanding any special explanation. Similar diversity is probably to be found among the wild relatives of all our cultivated plants, as well as in the unselected stocks that have been domesticated by primitive peoples.[1] The only reason why the condition of diversity should seem strange or unexpected arises from the current opinion that wheat is a normally uniform, self-fertilized plant. The diversity of the wheat is only such as might be expected from the analogy of any other cross-fertilized plant, wild or domesticated.

RELATION OF CROSS-FERTILIZATION TO DISEASE RESISTANCE.

In addition to the general biological interest of diversity and cross-fertilization in the wild cereals, as already pointed out, these facts may have practical value from the standpoint of disease resistance. If cross-fertilization represents the normal ancestral condition of the wheat plant it is worth while to consider the possibility that absence of cross-fertilization involves a decline of vital efficiency. Lessened resistance to disease is one of the most general symptoms of weakened vitality in vegetative varieties, and the same is probably true of those propagated by continued self-fertilization.[2]

The form of the wheat rust that occurs on the barberry is now being considered as the sexual phase of the fungus. It has been suggested by Mr. W. T. Swingle that the pest may gain increased virulence through occasional crossing in the barberry stage and that the elimination of barberries and related plants from wheat-growing regions might result in an eventual weakening of the fungus by excluding crossing altogether.[3]

In addition to this possibility of mitigating the ravages of wheat rust by preventing the sexual reproduction, or at least the cross-fertilization, of the parasite, it is worth while to consider the possibility of securing and acclimatizing less susceptible varieties of wheat from primitive cross-fertilized stocks, if such really exist in Palestine or the neighboring regions. As often happens, the study of a question of general scientific interest may lead to a fact of practical agricultural importance. In learning something of the habits of the wild wheat a suggestion is gained regarding the behavior of the cultivated types of wheat.

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[1] Mr. Aaronsohn finds much less diversity in domesticated barley and a still smaller amount in wild barley.

[2] Cook, O. F. The superiority of line breeding over narrow breeding. Bulletin 146, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

[3] Mr. Aaronsohn states that wheat rust is destructive in some years, though there is no Berberis in Palestine. Experiments to test the relation of the sexual phase of rust fungi to virulence have been reported by Freeman and Johnson in Bulletin 216 of the Bureau of Plant Industry p. 33–45. In two years 52 generations of uredospores were grown without any appreciable diminution of vigor.

It is now regretted that this possibility of securing disease-resistant varieties by acclimatizing the domesticated wheat of Palestine in the United States did not suggest itself until a day or two before leaving the neighborhood of Mount Hermon, where the most extensive diversity and other indications of cross-fertilization were observed. The apparently complete absence of rust on the wild wheat finally suggested a comparison in this regard with the cultivated wheat and brought to light the fact that the domesticated wheat was also free from rust. Rust was looked for in all of the fields that were afterwards visited, but with the same negative result so far as that district was concerned. The next day, down in the Jordan Valley, a few rusted stalks were seen, and a week afterwards between the Jewish colonies of Hedera and Petach Tikwa, to the south of the Plain of Sharon, a little rust was found in wheat that seemed distinctly inferior to that of the Mount Hermon district. Most of the wheat of the lower altitudes was already harvested.

FIG. 5.—Head of a large-seeded variation of wild wheat. (Natural size.)

Of course, there may be other reasons for the absence of rust quite apart from any quality of resistance the native varieties of Palestine may possess. A small planting of wild wheat at San Antonio, Tex., in the spring of 1911, that was severely attacked by rust shows that the plant has no complete immunity. But whatever the reasons for the apparent resistance to the rust, they are likely to prove interesting in the United States, where the most serious damage from rust fungi seems to occur in the parts of the country where the climate is warm, like that of Palestine. Indeed, the wild wheat has been found by Mr. Aaronsohn to extend along the desert mountains to the east of the Jordan Valley almost to the shores of the Dead Sea, a region that resembles the Salton Sink of California, not only in lying below the level of the sea, but also in its climate, physical features, and to a certain extent in its specialized

desert vegetation. Yet in Palestine neither the wild nor the domesticated wheat is excluded by these extreme conditions. A German company is engaged in shipping wheat in boats across the Dead Sea to be carried up to Jerusalem by donkeys or camels. European settlers are beginning to establish themselves about Jericho, in the region that visitors from California are likely to look upon as the Imperial Valley of Palestine.

RELATION OF DIVERSITY TO ACCLIMATIZATION AND ADAPTATION.

Diversity is quite as important a factor in acclimatization and adaptation as in the breeding of new varieties. Breeders often resort to the crossing of varieties as a means of arousing some of the latent diversity of characters that has been suppressed by selection, in order to secure materials for further selection. In dealing with a diverse type that has never been reduced to uniformity by selection it is not necessary to begin by crossing, for a wealth of normal variation is already at hand. As much diversity may be expected in characters that give adaptation to external conditions as in the forms and color of the heads and other external features that serve to distinguish varieties.

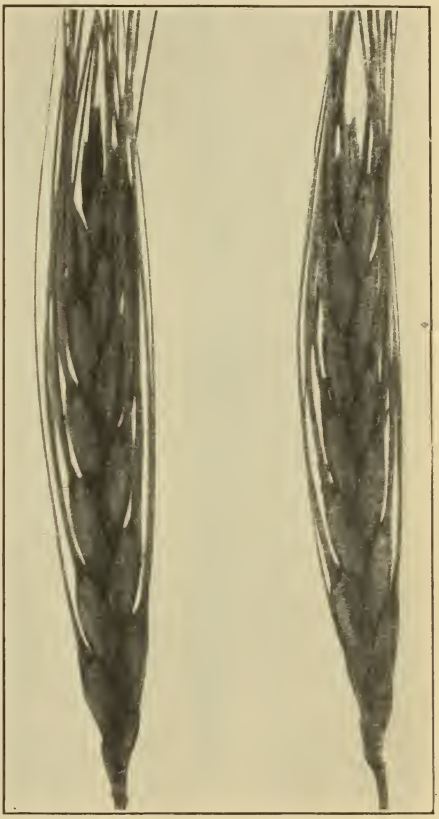

FIG. 6.—Nearly mature heads of wild wheat, ordinary form, to compare with figure 8. (Natural size.)

The facts of diversity and the indications of cross-fertilization in these primitive and apparently rust-free stocks of wheat lend them special interest from the standpoint of acclimatization. Experiments with such stocks should make it possible to ascertain the full range of their possibilities of adaptation to special conditions of climate and soil. Even though the primitive and very diverse stocks should appear inferior to the more uniform stocks that could be obtained from localities where a certain amount of separation of varietal types

has taken place, experiments with the diverse stocks might still be worth while as giving a better opportunity to test the full range of adaptation to different local conditions in the United States.

The range of acclimatization and adaptation in carefully selected uniform varieties is often very narrow. The members of such a variety represent the expression of only one set of characters corresponding to the characters of a single individual in a normally diverse stock. The function of selection is to regulate the expression of characters. Those lines of descent are preserved that bring the desired set of characters most uniformly into expression and keep latent all the undesirable characters. From the standpoint of the breeder any plant that shows a departure from the desired set of characters appears abnormal and is rogued out of the variety. To limit selected stocks as nearly as possible to the progeny of single individuals is the most effective method of preserving uniformity in the expression of characters. Thus a carefully selected variety may be said to have only an individual range of adaptation. As long as the variety is kept uniform its possibilities of adaptation are no greater than those of the original parent of the strain.

FIG. 7.—Side view of heads of wild wheat of ordinary form, shown in figure 6, to compare with figure 9. (Natural size.)

Diversity is likely to be aroused when a variety is transferred to new and unwonted conditions. Some of the reversions may prove better adapted to the new conditions than the parent variety, but there seem to be cases where little or no progress is made toward better adaptation. These artificial limitations are avoided when normally diverse stocks can be used instead of the chance variations of selected strains that may represent, after all, only a small part of the adaptive possibilities of the species.

The use of the more diverse stocks for purposes of acclimatization also promises a great saving of labor and expense in conducting experiments. If the same or a greater range of possibilities of adaptation can be secured by plantings of a single diverse stock as from large numbers of selected varieties, much of the costly repetition of local tests of large numbers of varieties may be avoided. It is necessary

in most crops to isolate and make comparative tests of the most promising individual strains that become acclimatized, but this is vastly easier than to maintain separate plantings and selections of the large numbers of different stocks that are often brought together in variety tests.

SUPPRESSION OF ADAPTIVE CHARACTERS BY SELECTION.

Most of the careful selection that has been applied to wheat has been done in the different countries of northern Europe, in relatively cold, moist climates and with soil conditions unlike those of many of the wheat-growing regions of the United States. It is true that some useful importations have been made from Turkey and Russia, but even in such cases there could be no assurance that the selection that had been given to these varieties was calculated to secure the strains best adapted to our conditions. On the contrary, it is quite possible that the selection applied to the wheat plant in Europe, instead of improving it for our purposes, may have tended to suppress some of the characters that are needed to secure a full measure of adaptation in the United States. Characters that could be of the greatest importance in Kansas, Texas, or Arizona might be of no use in northern Europe and may have been suppressed by selection, even without any recognition of their existence. The strains that might be the best for our purposes may have been dropped out before the selected stocks reached the United States.

FIG. 8.—Nearly mature heads of a large-seeded variation of wild wheat, to compare with the ordinary form as shown in figure 6. (Natural size.)

The extension of the wheat crop into northern climates may explain the suppression of cross-fertilization, as suggested in a previous

chapter. With rain or cold weather at the time of flowering only the self-fertilized plants might be able to secure pollination and set their seeds. While mere absence of the conditions of sunshine, heat, and dryness that may be required for the opening of the glumes or exsertion of anthers might not bring about a suppression of these characters, the repeated elimination of all of the plants that required cross-fertilization would constitute a very effective form of unconscious selection by unfavorable weather conditions. The tendency would be to place all the northern varieties on a basis of self-fertilization. Mr. W. T. Swingle suggests the possibility that the greater vigor and disease resistance of the so-called durum wheats may be due to a retention of the habit of cross-fertilization, as well as to better adaptation to dry climates. If more vigorous individual strains resulted from occasional crossing they would gradually take the place of the others, especially if they proved more resistant to rust or other diseases. As yet there is no definite indication of how long a variety of wheat may be expected to maintain its vitality on a basis of strict self-fertilization. Even the idea of securing improved strains by isolation of the progenies of superior individual plants dates back only about a century, as already stated.

FIG. 9.—Side view of the heads of a large-seeded variation of wild wheat as shown in figure 8, to compare with figure 7. (Natural size.)

Though a cross-fertilized type of wheat might be valuable by reason of greater vigor, productiveness, or disease resistance, such a type would doubtless be more difficult to keep in uniform condition than a self-fertilized variety. Cross-fertilized varieties of wheat would probably require the same persistent attention that must be given to varieties of cotton and other cross-fertilized plants in order to establish and maintain a uniform expression of the characters. But even with the self-fertilized varieties continual reselection is needed to eliminate the degenerate individuals and lines of descent. This is shown by the favorable results that are nearly always reported from such experiments. The stronger the tendency to degeneration the more beneficial the effects of reselection will appear, for there are more of the inferior lines to eliminate.

The difficulty of securing uniformity of expression stands in the way of utilizing hybrids for the commercial culture of cotton, and the same factor is likely to be encountered with any open-fertilized wheat hybrids that might be produced. But there is no particular necessity that wheat kernels be exactly alike, if larger yields can be obtained from diverse cross-fertilized stocks. Millers often mix two kinds of wheat together to produce particular grades of flour. The importance of the crop is such as to warrant full investigation of any biological factors that seem to open the way of improvement. The factor of diversity enlarges the possibilities of adaptation to a wider range of natural conditions.

A LARGE-SEEDED VARIATION OF WILD WHEAT.

After the previous chapters of this report had been written another outdoor planting of the wild wheat was made, this time in southern California. The results were altogether different from those of the previous experiment in Texas, where the wheat made only a scanty growth and became badly infested with rust. The California planting was made at the United States Experiment Farm at Bard, Imperial County, in the Colorado River Valley, a few miles below the Laguna Dam. A first sowing, in November, was more successful than others made at later dates. The plants grew vigorously during the winter months, attained a larger size, and produced finer heads than any that were seen in Palestine. (See Pl. XII.) Instead of being limited to 15 or 20 stalks, as in Palestine, the California plants produced clusters of 50 stalks and upward. Owing to the very abundant stooling, the ground was covered with a dense mass of herbage, suggesting a possible value for forage purposes. (See Pl. XIII.) The heads began to appear early in April and some of the seed was ripe a month later. As the season of 1912 was unusually late the ripening date would probably have been three or four weeks earlier in an ordinary year.

The same general range of individual diversity appeared in California as in Palestine, though the differences became more obvious with the larger size of the plants and the better development of the heads. But in one noteworthy instance the range of variation extended quite beyond anything observed in Palestine. The plant was somewhat larger than the others and with broader leaves. It produced about 90 stalks, though only about 60 heads were secured, the others having been eaten off, probably by a marauding burro. The heads were much broader, thicker, and more compact than those of the ordinary wild wheat. (See figs. 5, 6, 7, 8, and 9.) The most important character of the new form was the larger size of the kernels. Though these were only a little longer than the kernels of the other

plants, they were much thicker and broader. The size of the kernels is shown in figure 10, *B* in comparison with those of the ordinary wild wheat (fig. 10, *A*) and the so-called Sonora wheat that is usually planted in the Southwest (fig. 10, *C*). The weight of the individual kernels in the samples shown in figure 10, *A*, *B*, and *C*, averaged, respectively, 0.032 gram, 0.071 gram, and 0.038 gram, showing that the kernels of the large-seeded variation were about twice as heavy as those of the ordinary wild wheat or of the cultivated wheat growing in the same place. The average of 381 kernels of the same stock of imported seed which was used in sowing the experimental plat at Bard was only 0.022 gram per kernel, or only about one-third as heavy as the kernels of the new variation. (See p. 22.) The average weights of thoroughly dried kernels of 13 heads of the variation ranged from 0.054 gram to 0.073 gram with a general average of

FIG. 10.—Wheat kernels. *A*, Wild wheat, showing usual size; *B*, large-seeded variation of wild wheat; *C*, Sonora wheat grown in the same locality at Bard, Cal. (All natural size.)

0.062 gram for a total of 318 kernels. The average number of kernels per head was 24.46.

The seeds are not only larger than those of the ordinary wild wheat but are more uniform in size. Each spikelet contains two full-sized kernels instead of one large and one small kernel as in the wild wheat. Moreover, there are indications of a tendency toward a further increase of the number of kernels in a spikelet, for three of the heads had one or more of the spikelets with three kernels instead of only two.

Several other differences may be considered as consequences of the larger size of the kernels. Spikelets with two or three broad seeds become, of necessity, much wider than those that contain only one or two of the narrow, slender seeds of the wild wheat. The glumes of the broad spikelets not only spread farther apart, but are of a somewhat different shape. Perhaps as a result of greater pressure exerted by the broad seeds in the younger stages of growth, the

glumes become more convex or gibbous, that is, more like those of domesticated types of wheat. (See Pl. XIV.)

The greater divergence of the glumes also appears to be responsible for a stronger curvature of the awns near the base, to bring them into line with the rachis. (Pl. XV.) Such curvature might easily result from increased pressure to which the thicker heads would be subjected in the leaf sheaths in which they are inclosed during the younger stages of growth. The presence of many crumpled awns also indicates that the broad heads experience unusual difficulties in emerging from the sheaths. Figure 11 shows one of these crumpled awns on one of the lower spikelets.

FIG. 11.—Head of a large-seeded variation of wild wheat, with spikelets falling apart. (Natural size.)

The greater pressure and increased friction of the broad heads in the leaf sheaths may also be responsible for differences in the rachis. The joints of the rachis of the broad-seeded variation are shorter, thicker, and more curved than those of the ordinary wild wheat.

That so many differences in the spikelets and rachis should arise as direct mechanical results of increasing thickness of the seed seemed rather improbable when the idea at first suggested itself, but parallel differences were found to occur in the domesticated types of wheat. In some of the so-called Sonora wheat growing in a neighboring field it was noticed that some of the heads had small, narrow spikelets near the base. Such spikelets not only had the same general shape as those of the wild wheat, but had the glumes straight sided and fitted together in the same way as in the wild wheat. Even more interesting was the fact that these narrow spikelets were accompanied by a marked elongation of the joints of the rachis, much as in the wild wheat.

Still another difference of the broad-seeded variation of the wild wheat may be considered as a mechanical change. Supposing that

the rachis has to be shortened and stiffened to force the thicker heads out of the leaf sheaths, this might explain a loss or reduction of another specialized feature, the jointed structure of the rachis. In any event, the large-seeded variation, with its broader and shorter heads, shows a distinct tendency toward a firm rachis. Some of the terminal joints are ready to separate as soon as the heads are mature, as in the wild wheat, but there is a much greater tendency for half of the head to remain together. (Fig. 11.) Many of the heads remained quite unbroken until after they were picked and thoroughly dried out. Indeed, there seemed to be a difference in this respect between the individual heads of the large-seeded plants. Those that were longer and more open, like those of the wild wheat, seemed to have a more fragile rachis than the shorter and more compact heads.

The importance of the new variation as a step in the acclimatization of the wild wheat will depend, of course, on the constancy of the characters, which must be determined by planting the seed and raising the progeny. But whatever its nature or cause, the existence of such a variation is a significant fact, for it shows that other departures from the wild type are to be expected. If the plant represents a definite variation a few more changes of similar magnitude would mean the production of a cereal of agricultural value. But there can be no assurance regarding the behavior of the variation until further generations have been grown.

Considered even as a natural hybrid with the domesticated wheat in Palestine, the plant would be interesting as a further evidence of cross-fertilization. But the jointed rachis and other characters do not favor the idea of hybrid origin. An alternative possibility is that the variation was present in the seed that was planted and is to be considered merely as an extension of the already very wide range of variation known to exist in the wild wheat in Palestine. If this be true, it becomes the more important to know the complete range of variation of the species in its natural state. Other forms of equal or greater interest might be found. A third possibility is that a new variation has been induced by transferring the plant to the new conditions to which it was exposed in southern California. All of the remaining seed of the imported stock was sorted over carefully, but nothing was found that in any way resembled the broad spikelets of the large-seeded variation. But this affords no conclusive proof that an ordinary narrow spikelet gave rise to the new variation. It would be necessary to make a thorough search of the district from which the seed came before it would be safe to conclude that a new variation had been induced by the transfer to California.[1]

[1] Mr. Aaronsohn is inclined to the opinion that the large-seeded variation represents a natural hybrid with the domesticated type of wheat, similar forms having appeared among his artificial crosses.

ECONOMIC PROSPECTS OF THE WILD WHEAT.

Whether the wild wheat of Palestine will have a direct agricultural value, in addition to the light thrown upon general problems of heredity and breeding, is still doubtful. For reasons already explained, the plant is not well adapted to cultivation as a grain crop in its present form and can scarcely be utilized in this way unless varieties can be developed with heads that hold together instead of falling apart into separate spikelets, as shown in figure 11.

Apart from its possibilities of developing into a cereal, the ability of the plant to maintain itself in extremely rocky soils might give it value as a winter pasture grass in some of the dry regions of the Western States, especially in limestone districts. The firm, indehiscent, well-armed spikelets would undoubtedly protect the seed against many small birds and insect enemies that would interfere with the natural propagation of any ordinary large-seeded cereal grass and might enable the wild wheat to maintain and extend itself naturally when once established in favorable places. On the other hand, a careful study of the habits of the plant should be made before giving it any opportunity to escape from cultivation. Though nothing was noticed in Palestine to indicate such a danger, it is not inconceivable that the wild wheat might, under some conditions, invade cultivated lands and become an undesirable weed. It is a well-known fact that harmless plants sometimes become harmful weeds when introduced into a new country.

In a level region with strong winds the spikelets of the wild wheat might be blown long distances and then bury themselves in the ground, to wait indefinitely until rain or irrigation gave opportunities for germination. The plant would probably behave in the entire southwestern region strictly as a winter annual, and this would doubtless make it very easy to eradicate from any cultivated land.

The wide range of diversity manifested by the wild wheat makes it evident that the full possibilities of utilizing the species are not to be determined without a much wider and more thorough study. Unless the range of variation of the species is known there can be no estimate of the possibilities of selective improvement. Even from the standpoint of historical and biological interest it is worth while to determine whether such types as the domesticated wheats or emmers can be secured by selection from this wild species.

There is also the possibility pointed out by Mr. Aaronsohn of utilizing the wild wheat in making useful hybrids with domesticated types. As this work is now in progress at the Jewish Agricultural Experiment Station at Haifa, Palestine, some indication of its pros-

pects can probably be gained within two or three years. Though hybrids seem to be much less useful in field crops than in horticultural plants, they are likely to have more value in plants capable of regular self-fertilization like wheat than in those that remain open to continuous crossing, as in the case of cotton. It is not yet known whether crosses of the wild wheat with domesticated varieties would be adapted to self-fertilization, but there is a fair prospect of Mendelian results in such cases where a desired character represents an absence or failure of expression of a specialized feature, such as the joints of the rachis or the mechanism that opens the glumes of the wild wheat.

The chief advantages that are to be sought by the making of such hybrids are increased vigor, fertility, and rust resistance. No indications of rust or other diseases were found in the wild wheat in Palestine or in the very diverse cross-fertilized stocks of the domesticated wheat. Though this apparent immunity may have been due to other causes, the possibility of an inherent difference in this respect between self-fertilized and cross-fertilized forms is worthy of consideration. The acclimatization of cross-fertilized varieties of wheat may open the way to a regular utilization of the increased vigor and fertility that appear in artificial hybrids between self-fertilized varieties.

CONCLUSIONS.

As the wild wheat of Palestine is of interest from different standpoints it may be convenient to have separate summaries of the facts relating to the various aspects of the subject.

CHARACTERS AND HABITS OF WILD WHEAT.

The wild wheat is widely distributed on the slopes of the Anti-Lebanon range of mountains in northern Palestine and Syria, where it behaves as a truly indigenous plant. The finding of the same plant under very different conditions in the Jordan Valley, as reported by Mr. Aaronsohn, indicates that it is not localized about Mount Hermon, but probably has a much wider natural distribution, yet to be delimited.

The wild wheat is especially abundant on limestone formations, where it often appears as the dominant grass. On the volcanic areas that are often abruptly intruded among the limestones the wild wheat is usually absent or is represented by only scattering individuals. The causes of this apparent limitation of the wild plant are not yet understood.

The wild wheat comes to maturity in the spring, at the same time as the domesticated wheat. At the end of June, in the season of 1910, nearly all the plants had passed the flowering stage and on many of them the seeds were fully mature and beginning to fall. The plants that grew in moist places or in the plowed fields were somewhat later than the others and showed a distinct tendency to successive development of the heads, some of which were still in the flowering stage.

In addition to the differences that could be ascribed to external conditions there was a notable diversity among the individual plants, especially in colors, spines, hairs, and bristles of the glumes. In the shapes of the heads the wild wheat showed much less diversity than the cultivated wheat of Palestine.

Adaptations for cross-fertilization were found in the wild wheat and also indications of similar characters in the primitive unselected stocks of the domesticated wheat grown in the same part of Palestine. Some of the flowers have their anthers exserted before the shedding of the pollen, and, conversely, in some flowers the glumes spread apart so that pollen is admitted before the anthers mature. The exsertion of the stamens allows the pollen to be scattered by the wind. The spreading of the glumes permits wind-blown pollen to reach the stigmas.

Indications of sexual dimorphism were found. Some of the plants had distinctly proterogynous flowers, with the stigmas exposed before the maturity of the anthers, while on other plants the flowers appeared to be proterandrous, the anthers being exserted while the stigmas were still only partly developed.

The production of seed in heads that have not emerged from the sheaths shows that some of the wild wheat is capable of self-fertilization, like the domesticated wheats. It is from such forms with simultaneous development of stamens and pistils that the self-fertilized wheat varieties of northern Europe may have been derived. The selection of proterogynous forms would afford a means of developing cross-fertilized varieties.

The joints of the rachis are highly specialized. They separate from each other at maturity, but remain permanently attached to the spikelet, forming beaklike organs barbed on each side with stiff bristles. The function of the specialized joints is to facilitate the movements of the spikelets, which creep into crevices of rocks or bury themselves in the soil. The strongly barbed awns also assist in the dissemination of the spikelets.

The spikelets never develop more than two seeds, often only one. The seeds of the same spikelets are usually unequal and the smaller

one usually fails to germinate. The smaller seed is produced by the lower flower of the spikelet, which has the larger awn.

The seedlings usually germinate with three radicles, which emerge from both faces of the spikelet. Four or five radicles sometimes appear.

The finding of spikelets with intermediate characters between the wild wheat and Aegilops indicates the formation of natural hybrids.

THE PROBLEM OF THE WILD PROTOTYPE.

Though there is no reason for any further doubt of the existence of a wild type of wheat in Palestine, equal certainty can not be claimed for the idea that the Palestine wild wheat is the ancestor or true prototype of the domesticated types of wheat. It is still doubtful whether all the cultivated types of wheat arose from a single wild species or from different species.

The wild wheat of Palestine shares some of the characters of emmer (*Triticum dicoccum*) and einkorn (*Triticum monococcum*), but should be considered as a distinct new species, to which the name *Triticum hermonis* may be applied, in allusion to its native habitat on the slopes of Mount Hermon.

A very diverse unselected stock of domesticated wheat (including forms referable to *Triticum aestivum* and *T. durum*) is cultivated in the region of Mount Hermon and grows frequently as a spontaneous or escaped plant. But even in its most degenerate condition the cultivated type of wheat shows no tendency to revert or approximate to the characters of *Triticum hermonis*. Some of the depauperate plants gave indications of the same habits of cross-fertilization as in the wild wheat.

Though the wild wheat of Palestine possesses all the characters that the European specialists expected to find in the primitive ancestor or prototype of the domesticated wheat, these characters might also be expected to occur in any wild relative of the wheat plant and do not afford ground for a final conclusion regarding the relationships that exist between the wild wheat of Palestine and the domesticated cereals.

The economic value of this new wild relative of the cultivated wheats does not depend on its being the original progenitor or prototype. Its relationship is at least close enough to permit crossing or to justify an attempt at developing new types of cereals adapted to special conditions, such as those of our Southwestern States.

FACTORS OF HEREDITY AND BREEDING.

The wild wheat of Palestine shows a wide range of individual diversity (heterism), like the wild relatives and unselected stocks of

other domesticated plants. This condition of diversity is to be explained by the presence of specialized adaptations for cross-pollination, as well as by the absence of methodical selection.

The cultivated wheat of Palestine shows the same condition of individual diversity as the wild wheat and retains the same facilities for cross-pollination by the exsertion of the anthers and the spreading of the glumes. Instead of being naturally restricted to self-fertilization, the wheat plant seems to have been specially adapted for cross-fertilization in a dry climate.

The condition of self-pollination found among domesticated wheats is not a primitive condition but has been reached through a reduction or loss of adaptations for crossing, like those possessed by the wild type. Though in some of the domesticated varieties the cross-fertilizing adaptations may have been completely lost, certain forms of domesticated wheat still remain capable of natural crossing in the same manner as the wild wheat.

The habit of self-fertilization found among our cultivated varieties of wheat is no longer to be considered as an original ancestral condition. Analogies with other plants suggest that an eventual decline in vigor, fertility, and disease resistance may be expected in varieties of wheat that are limited to self-fertilization.

AGRICULTURAL APPLICATIONS.

The wild wheat of Palestine is a hardy plant, in the sense of being able to exist under a wide range of natural conditions. Its natural distribution extends from the higher slopes of Mount Hermon, that are covered with snow in the winter, to the parched walls of the Dead Sea Valley.

The behavior of wheat in Palestine suggests the possibility of acclimatizing new types of wheat adapted to arid subtropical districts of the Southwestern States. This possibility relates not only to the wild wheat, but to the primitive unselected stocks of wheat that are grown in arid subtropical districts of Palestine and adjacent regions.

The native wheat fields of Palestine produce excellent crops in spite of the fact that the individual plants show a wide range of differences, as bearded or beardless heads, very open or closely crowded spikelets, white, red, or black chaff, with smooth, pruinose, or velvety surfaces, dark or light grains, etc., from which an endless number of varieties could be separated by selection.

The occurrence of this primitive diversity under conditions that admit of normal cross-fertilization indicates that the same method of acclimatization can be applied to wheat as to diverse types of cotton or other cross-fertilized crop plants. The full range of adaptation of a widely diversified type can be obtained, instead of the limited

possibilities of self-fertilized strains selected on the basis of adaptation to entirely different conditions in northern Europe.

Consideration should also be given to the possibility of securing increased rust resistance in wheat by the acclimatization of more vigorous cross-fertilized types or by using such types or the wild species to produce hybrids with American varieties.

Cross-fertilized varieties of wheat would be subject to injury from wet weather at the time of flowering, but this danger would not be serious under the climatic conditions of the Southwestern States or of the Great Plains area.

There is also the possibility of utilizing the wild wheat as a self-sown forage plant, either in cultivation or by allowing it to escape and establish itself on grazing lands in California or other Southwestern States. In view of the fact, however, that the seeds are specially adapted for dissemination the possibility of the plant escaping and becoming a weed will have to be carefully considered before any general distribution can be advised, even for experimental purposes.

DESCRIPTION OF PLATES.

PLATE I. Wild wheat growing among nummulitic limestones in an uninhabited district between Rosh Pinar and the Lake of Gennesaret (Bahr Tabariyeh), Palestine. Photographed by Mr. Aaron Aaronsohn.

PLATE II. Situations where the wild wheat thrives. Fig. 1.—On Jebel Kanaan, above Rosh Pinar. Fig. 2.—Between El Hadr and Arny. Figs. 3 and 4.—Near Mejdel esh Shems. The first locality is west of the Jordan Valley, while the others are on the lower slopes or foothills of Mount Hermon. Photographed by Mr. Aaron Aaronsohn.

PLATE III. Spontaneous forms of domesticated wheat from volcanic soils at El Hadr, Palestine, where the spontaneous wheat was quite abundant. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE IV. Depauperate plants of domesticated wheat from cultivated fields on the slopes of Mount Hermon above Arny, adjacent to uncultivated lands where the wild wheat grows in abundance. (Natural size.)

PLATE V. Heads of wild wheat grown at Bard, Cal.; the larger head with anthers extruded, and the other with glumes spread at the time of flowering. The latter is seen from the side, and shows the extent to which the glumes open. Photographed by Mr. C. B. Doyle. Awns cut off before photographing. (Natural size.)

PLATE VI. Terminal spikelets of Aegilops and supposed hybrid between wild wheat and Aegilops. The terminal spikelets remain attached to each other, as in Aegilops, instead of separating as in the wild wheat. Photographed by Mr. C. B. Doyle.

PLATE VII. Spikelets of *Aegilops ovata* and supposed natural hybrid between Aegilops and wild wheat. Figs. 1 and 2.—*Aegilops ovata*, front and side views. Figs. 3 and 4.—Supposed hybrid, front and side views. From negatives by Dr. Albert Mann. (Magnified about 6 diameters.)

PLATE VIII. Local variety of wild wheat from Khan Jubb Yusef, Palestine, near the Lake of Gennesaret. All specimens from this locality had densely hairy glumes. Many of the spikelets have the awns nearly equal. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE IX. Local variety of wild wheat from the slopes of Mount Hermon, above Arny, altitude about 4,000 feet, showing narrow spikelets and smooth glumes. This plate may be considered as representing the type of *Triticum hermonis*. The awns are longer and more slender than those of the variety shown in Plate VIII, and are usually very unequal. Many of the spikelets have only one seed. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE X. A diverse stock of wheat grown by the Pima Indians near Sacaton, Ariz. Much of the so-called Sonora wheat of the Southwest is a mixture of varieties or a very diverse stock like the domesticated wheat of Palestine. Photographed by Mr. Rowland M. Meade.

PLATE XI. Diverse types of cultivated wheat from El Hadr, Palestine. This photograph indicates some of the color differences as well as the variations of form and structure. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE XII. Heads of an ordinary form of wild wheat grown at Bard, Cal. Three of the largest heads, much larger than any seen in Palestine. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE XIII. Wild wheat growing at Bard, Cal. Fig. 1.—Part of the experimental plat showing dense foliage. Fig. 2.—Heads of wild wheat in experimental plat. Photographed by Mr. L. H. Dewey.

PLATE XIV. Heads of a large-seeded variation of wild wheat, grown at Bard, Cal.; to compare with Plate XII. Photographed by Mr. C. B. Doyle. (Natural size.)

PLATE XV. Spikelets of wild wheat grown at Bard, Cal. Fig. 1.—Four spikelets of ordinary form of wild wheat, to show the narrow, oblong form and straight, unequal awns. Fig. 2.—Three spikelets of large-seeded variation, to show the broader and more rounded form and the equal awns, curved at base. Photographed by Mr. C. B. Doyle. (Natural size.)

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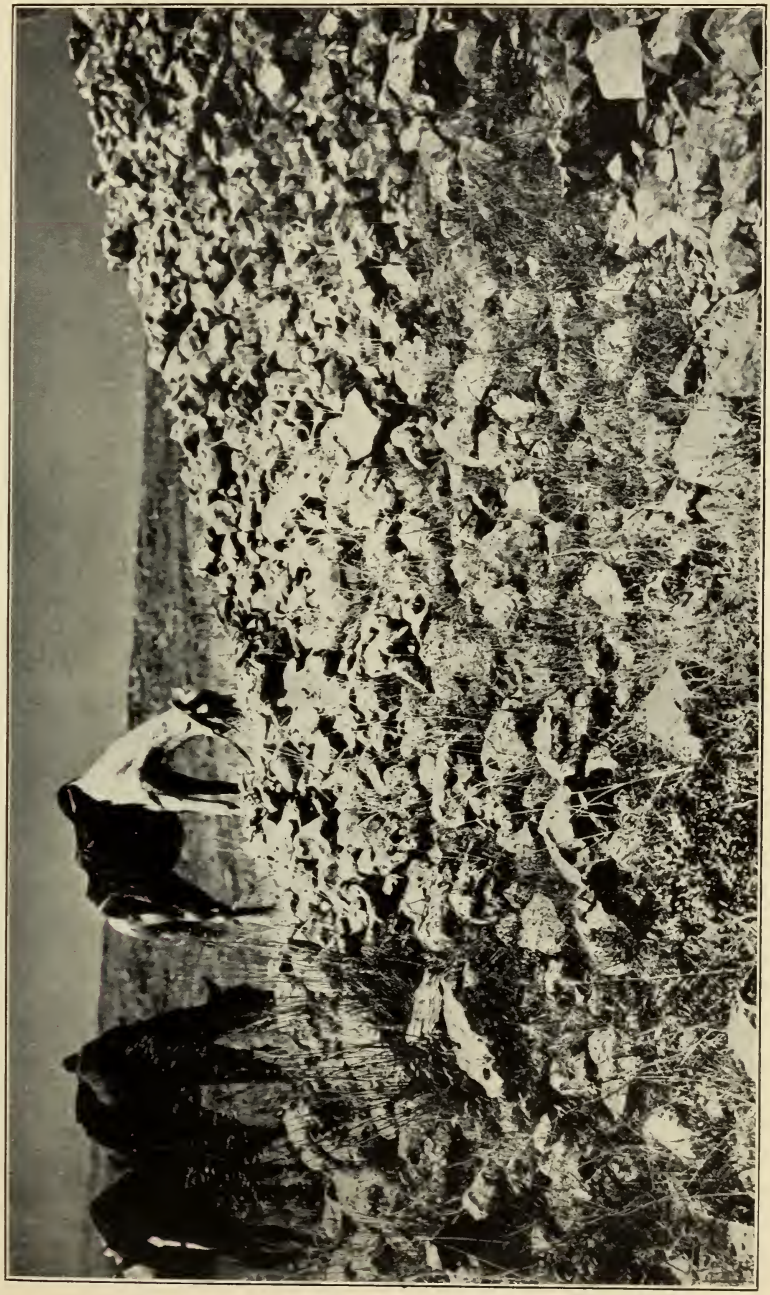
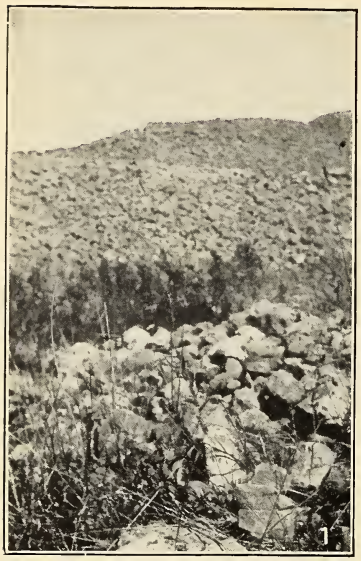
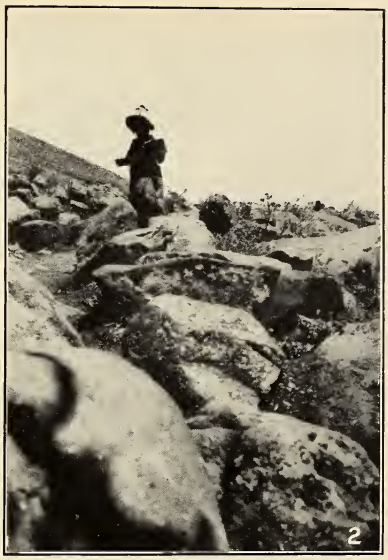
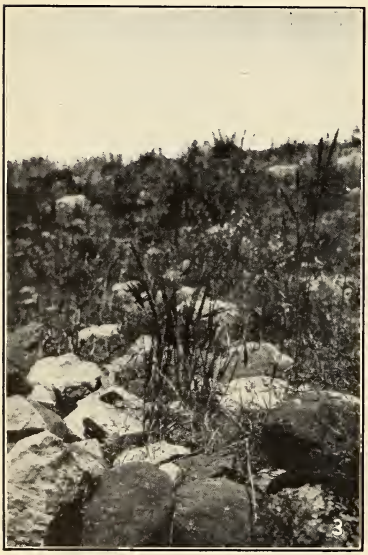
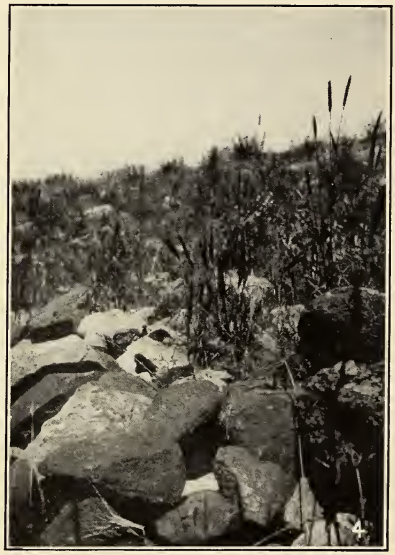


WILD WHEAT GROWING AMONG NUMMULITIC LIMESTONES, BETWEEN ROSH PINAR AND THE LAKE OF GENNESARET (BAHR TABARIYEH), PALESTINE.









SITUATIONS WHERE WILD WHEAT THRIVES.

FIG. 1.—ON JEBEL KANAAN, ABOVE ROSH PINAR.
FIG. 2.—BETWEEN EL HADR AND ARNY.
FIGS. 3 AND 4.—NEAR MEJDEL ESH SHEMS.

SPONTANEOUS FORMS OF DOMESTICATED WHEAT FROM VOLCANIC SOILS AT EL HADR, PALESTINE.

(Natural size.)

DEPAUPERATE PLANTS OF DOMESTICATED WHEAT FROM A CULTIVATED FIELD ON THE SLOPES OF MOUNT HERMON ABOVE ARNY, ADJACENT TO WILD WHEAT.

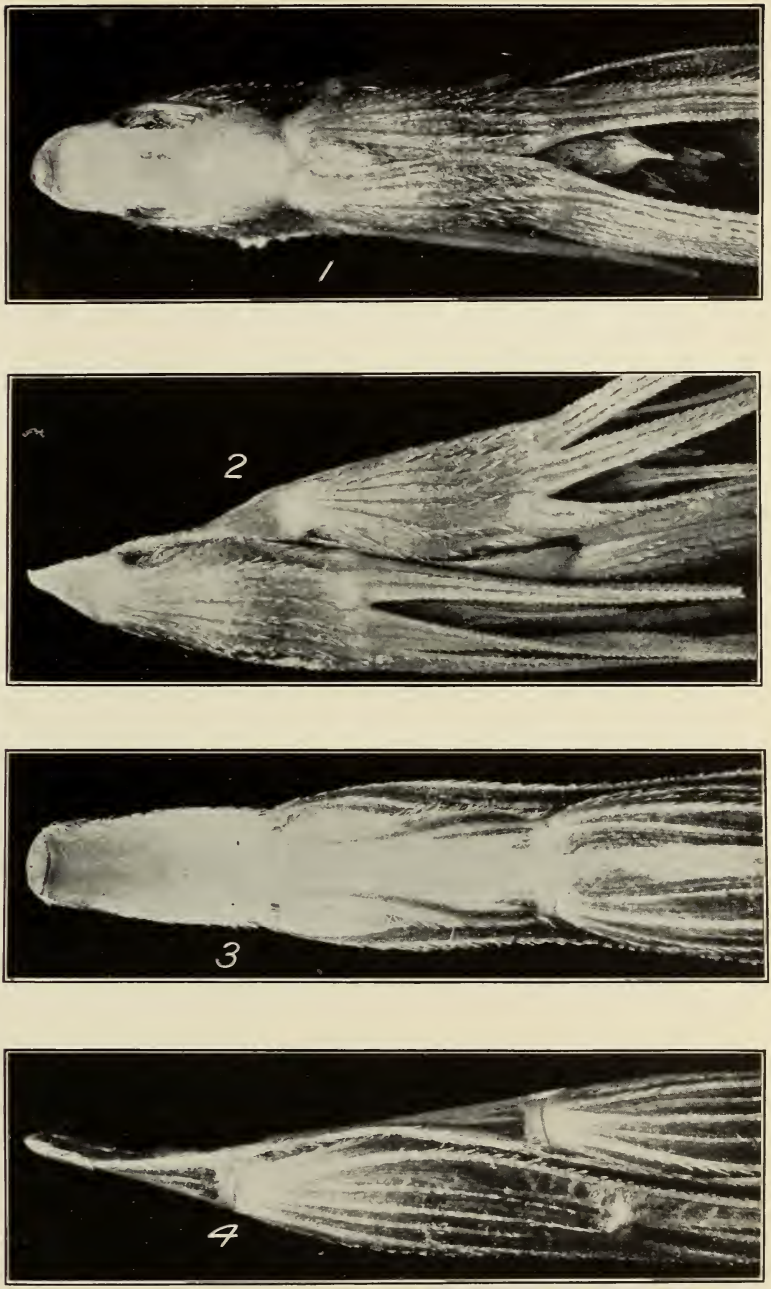
(Natural size.)

HEADS OF WILD WHEAT GROWN AT BARD, CAL., WITH ANTHERS EXTRUDED AND GLUMES SPREAD AT THE TIME OF FLOWERING. AWNS CUT OFF BEFORE PHOTOGRAPHING.

(Natural size.)

TERMINAL SPIKELETS OF AEGILOPS (*A*) AND SUPPOSED HYBRID BETWEEN WILD WHEAT AND AEGILOPS (*B*).

(Magnified nearly 2 diameters.)



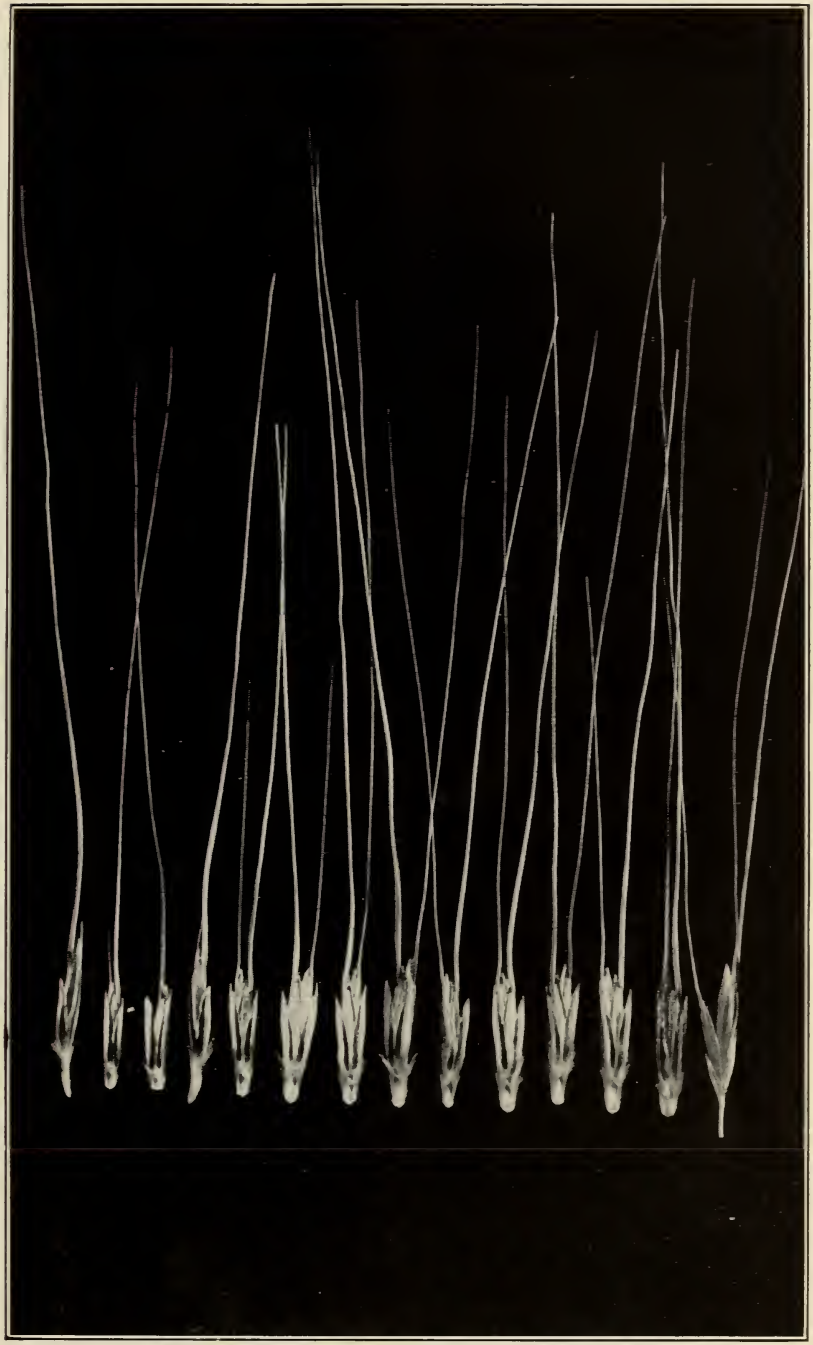
SPIKELETS OF AEGILOPS OVATA AND SUPPOSED NATURAL HYBRID BETWEEN AEGILOPS AND WILD WHEAT.

FIGS. 1 AND 2.—AEGILOPS OVATA, FRONT AND SIDE VIEWS.
FIGS. 3 AND 4.—SUPPOSED HYBRID, FRONT AND SIDE VIEWS.

(Magnified about 6 diameters.)

LOCAL VARIETY OF WILD WHEAT FROM KHAN JUBB YUSEF, PALESTINE, NEAR THE LAKE OF GENNESARET, SHOWING DENSELY HAIRY GLUMES.

(Natural size.)



LOCAL VARIETY OF WILD WHEAT FROM THE SLOPES OF MOUNT HERMON, ABOVE ARNY, ALTITUDE ABOUT 4,000 FEET, SHOWING NARROW SPIKELETS AND SMOOTH GLUMES.

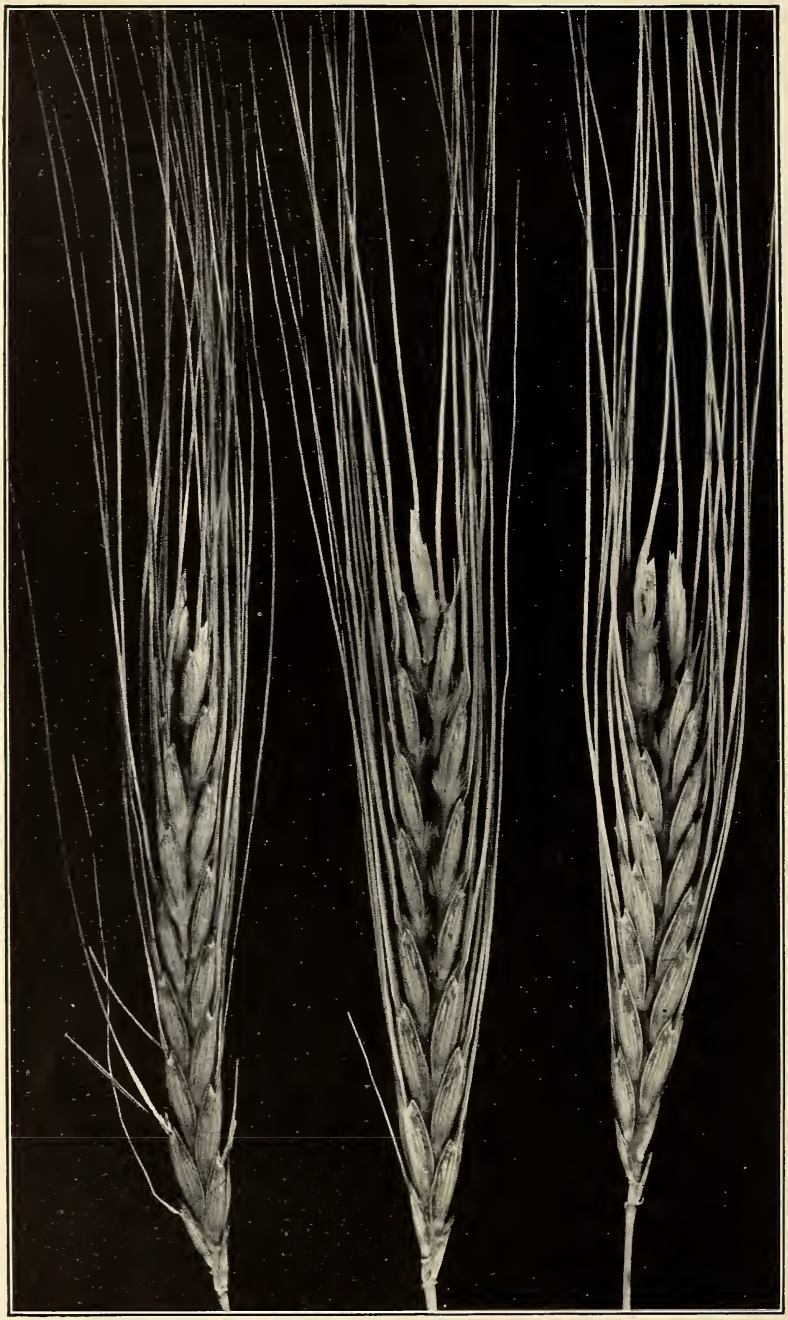
(Natural size.)

A DIVERSE STOCK OF WHEAT GROWN BY THE PIMA INDIANS NEAR SACATON, ARIZ.

(Natural size.)

DIVERSE TYPES OF CULTIVATED WHEAT FROM EL HADR, PALESTINE.

(Natural size.)



HEADS OF AN ORDINARY FORM OF WILD WHEAT GROWN AT BARD, CAL.

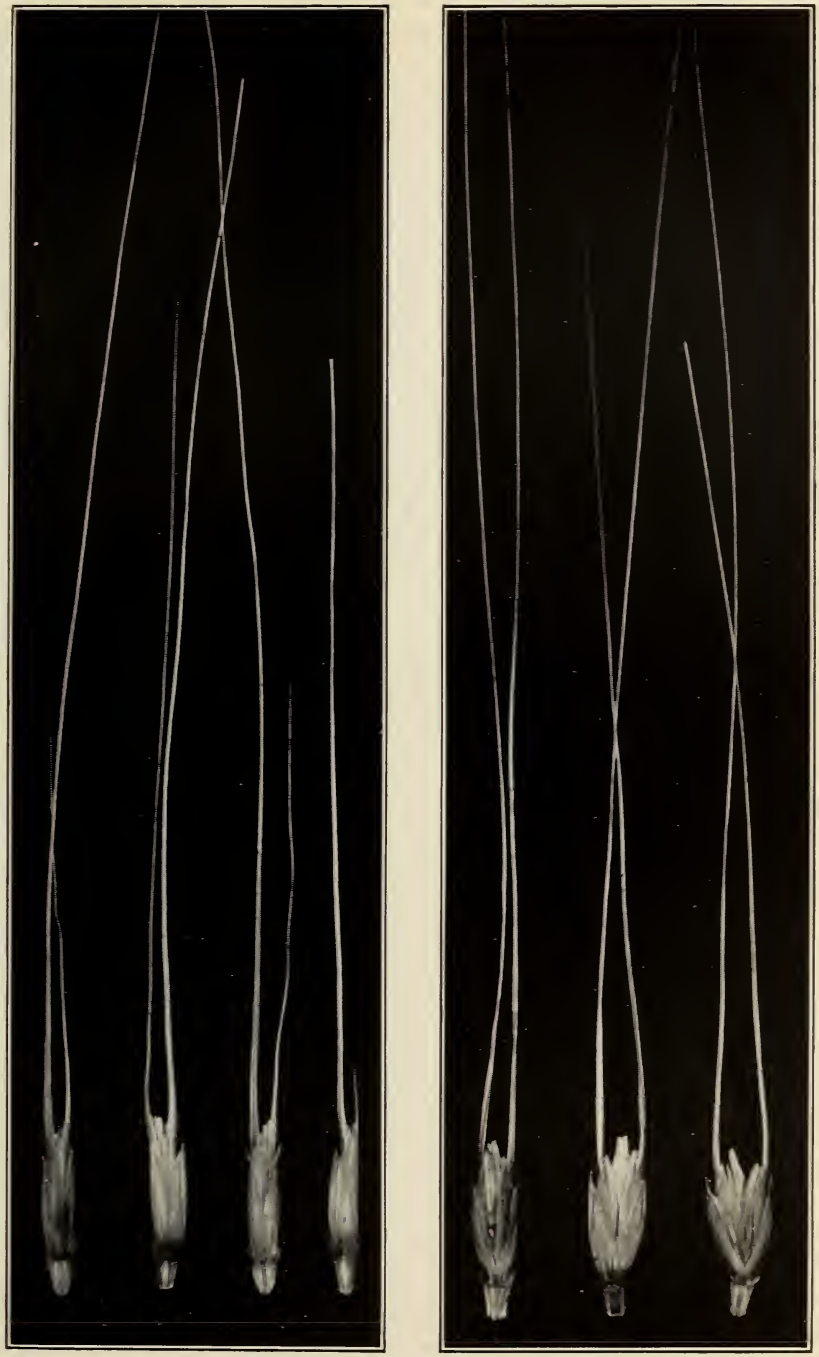
(Natural size.)

FIG. 1.—PART OF THE EXPERIMENTAL PLAT OF WILD WHEAT AT BARD, CAL., SHOWING DENSE FOLIAGE.

FIG. 2.—HEADS OF WILD WHEAT IN EXPERIMENTAL PLAT AT BARD, CAL.
(Photographed by Mr. L. H. Dewey.)

HEADS OF A LARGE-SEEDED VARIATION OF WILD WHEAT GROWN AT BARD, CAL.

(Natural size.)



SPIKELETS OF WILD WHEAT GROWN AT BARD, CAL.

FIG. 1.—FOUR SPIKELETS OF ORDINARY FORM OF WILD WHEAT.
FIG. 2.—THREE SPIKELETS OF LARGE-SEEDED VARIATION.

(Natural size.)